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DIRECTIONAL PERMEABILITY OF SEASONED WOODS TO WATER AND SOME FACTORS WHICH AFFECT IT[1]

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INTRODUCTION

The study of wood permeability is a comparatively recent innovation in the field of scientific research. Investigations on plants elucidated the finer structure of woody stems, which in turn has led to speculation on the probable mechanism of liquid movement in wood.

The earlier investigations on fluid penetration into wood were made by those who were interested in the preservative treatment of wood. Subsequent research has been conducted on a much broader basis and has employed various methods of attack of a physical and chemical nature in an attempt to arrive at fundamental principles of wood permeability as well as improvements in various industrial aspects of the treatment of wood. One conclusion which stands out from a survey of the literature and from work in the field, is that the flow of liquids through wood is a complicated problem influenced by numerous factors, some of which are inherent in the structure of wood while others arise from the relationship of wood to the properties of a liquid.

Previous investigations by the authors represented an attempt to clarify certain controversial points concerning the effect of various treatments and liquids on wood permeability and to obtain a more complete knowledge of the comparative longitudinal permeability of woods.

Very little work has been done on the measurement of the rate of liquid flow through wood radially and tangentially, although information on the relative penetrance from impregnation studies has been reported. Since such permeability, or the lack of it, is important in many commercial uses of wood and in processes involving contact and penetration of liquids, information to aid in a fuller understanding of the subject seemed desirable. Accordingly a study of radial and tangential permeability of a number of woods was made with attention being given also to the comparative permeability of springwood and summerwood and of heartwood and sapwood in the two directions where possible.

REVIEW OF LITERATURE

In order to explain the penetration of preservative fluids into wood, Tiemann (*27*) [2] advanced the hypothesis that when wood was seasoned below the fiber-saturation point, narrow microscopical slits developed in the walls of the fibers and tracheids which rendered them penetrable to liquids. In common with the botanists of his time, he believed that the cells of wood in the green state were enclosed by a continuous

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[2] Reference is made by number (italic) to Literature Cited, p. 744.

primary wall through which liquid might pass but only very slowly even at high pressure. The difficulty of injecting air and preservative oils seemed to substantiate this.

Weiss (*28*) observed that there was greater penetration of creosote in the summerwood than in the springwood of the same annual ring in longleaf pine. This he explained by saying that the thick walls of the summerwood would crack more on drying than the thinner walls of the springwood.

On examination of creosoted blocks, Bailey (*1*) found that in most cases the secondary walls of the summerwood cells were unruptured and that even when ruptures occurred the primary walls remained intact. He also noted that air passed very readily through the dry springwood in which the walls were not checked. He observed (*2*) that carbon particles in suspension passed through unseasoned sapwood. From microscopic and photomicrographic studies he concluded that the pit membranes were not entire but had minute perforations in the thinner radii of the membrane. In studies on mercury penetration, Scarth (*16*) found that the mercury apparently passed to the adjoining tracheids through the pit membranes when the torus was in the normal, median position. When pits were absent or closed (aspirated) the mercury did not enter the cells.

From the results of penetration of a mercury sol and india ink into wood, Stamm (*18*) decided that if openings other than those in the pit membranes existed, they were too small to have an appreciable effect on the determination of membrane pore sizes. He found further that when the length of the effective capillaries between tracheids was taken as the thickness of the pit membrane (assumed to be approximately that of the middle lamella) in calculations to determine the size of the effective openings by electroendosmosis, the values approximated those obtained by hydrostatic methods. Very different values were found if the length of the capillaries was assumed to be the thickness of the cell wall. In a recent review, Stamm (*21*) states that the cell-wall permeability under pressure is negligible as compared to the pit-membrane permeability except in extremely resistant woods.

Much of the information on the effective capillary dimensions has been determined by Stamm. The methods which he has employed include electroendosmotic flow, hydrostatic flow, gaseous flow, overcoming surface tension in the capillaries, electrical conductivity, and permeability to colloidal sols.

The effective capillary cross section of some softwoods cut in the three structural dimensions was determined by electroendosmosis (*18*). By measuring the electrical conductivity of salt solutions in wood the ratio of the effective capillary length to the effective continuous capillary cross section was determined (*19*). By combining the data of the first method with that obtained by hydrostatic flow (pressure-drop method) the average effective diameter of the openings (calculated as circles) for the heartwood of two conifers was found to be from 11 to 23 mμ. The range in maximum effective diameters of five species was from 68 to 184 mμ (*18*). The average values obtained by a similar combination with electrical conductivity data (*19*) were later found to be in error owing to an invalid assumption. The maximum values were determined in all experiments by calculation from the pressure necessary to overcome the surface tension of the

water in the largest effective capillary. In the latter case (*19*) the maximum effective capillary radii were from 40 to 120 mμ for the heartwoods of several species and from 180 to 11,000 mμ for the sapwoods. Stamm (*20*) has suggested a method for determining the distribution of the size of openings in a membrane by the rate of change of the velocity of flow of air with changes in the effective capillary radius which varies with moisture content or relative humidity. The minimum effective capillary radius was determined by the departure from a linear relationship between moisture content and permeability to air at the appropriate relative humidity. The minimum effective radius for a tangential section of white pine heartwood was 10 mμ, the average radius 27 mμ, and the maximum radius 73 mμ.

The probable importance of aspirated pits on the penetration properties of wood has been emphasized by several investigators. Griffin (*7*), one of the earliest workers on this problem, determined by actual count the proportion of unaspirated and aspirated pits in seasoned and unseasoned Douglas fir for both the mountain and lowland types. The latter had relatively few aspirated pits in the green state as compared to the former. Air drying caused an increased number of aspirated pits in both the springwood and summerwood of the mountain type, whereas in the lowland type this occurred only in the springwood. Soaking the heartwood in alcohol before drying it prevented pitted aspiration.

Griffin (*7*, *8*) obtained a definite relation between creosote penetration in the wood and the proportion of unaspirated pits. Scarth (*16*) reported similar results or mercury penetration. MacLean (*13*) found a considerable proportion of aspirated pits in several woods, the springwood having a greater proportion of closed pits than the summerwood. He also believed this to be "at least partly responsible" for the difficulty of treating such woods.

Phillips (*15*) recently has studied the extent and time of occurrence of pit aspiration in five species of softwoods. The general conclusions already given were verified except that drying below the fiber-saturation point did not increase the number of aspirated pits. Pit aspiration increased gradually during the drying of green wood until nearly at the fiber-saturation point when almost all of the springwood pits became aspirated. The abrupt change indicated that aspiration was associated with the loss of the last traces of free water in the cells. The proportion of unaspirated pits was found to increase with increasing thickness of the cell wall when the diameter of the pits in the summerwood remained nearly the same. The average number of unaspirated pits per tracheid were from 0.5 to 6.3 for the springwood and from 2 to 11 for the summerwood in the air-dry wood.

Scarth and Spier (*17*) suggest that pit membranes are pulled over to the pit aperture because of resins and other colloidal material released into the tracheids at the time of the death of the living cells. The wood then becomes heartwood in character. Nonresinous conifers showed pit aspiration to a lesser degree, which also explained the greater permeability of their heartwood. Phillips (*15*) states that closure of pits may be caused by evaporation of the last drop of water in the pit cavity, causing the torus to be drawn gradually toward the pit aperture by the surface tension of the annular meniscus between the pit border and the torus. This may be true for drying

just above the fiber-saturation point, but it is doubtful whether it explains heartwood formation, for heartwood is not often at or below the fiber-saturation point.

Bailey (*2*) and Scarth (*16*) believe that the application of pressure probably forces the torus against the pit aperture, thus exerting a valvelike action and preventing the flow of liquid unless (*16*) the pressure is sufficient to rupture the pit membranes. Sutherland, Johnston, and Maass (*23*) and Buckman, Schmitz, and Gortner (*5*) found that permeability continued to increase with an increase in pressure with no sign of tapering off or decreasing as higher pressures were applied. Hence no valve action of the tori could have occurred. That the membranes had not been ruptured by pressure was shown by the fact that approximately the same curve was traversed by the stepwise reduction of pressure if adequate time was allowed for the attainment of an equilibrium rate of flow.

The comparative permeability of sapwood and heartwood is apparently characterized by a great variation for different species. No great amount of work has been done with specific intent to settle the question, but several reports give an approximate idea of what may be expected.

From tests on the relative ease of creosote impregnation of a number of conifers, Teesdale (*24*) found that the sapwood was more easily penetrated than the heartwood in those species possessing a highly developed system of resin canals. Species without resin canals were impregnated but little better in the sapwood than in the heartwood except in some woods with distinct color differences such as cedars, cypresses, etc. From impregnation studies on 25 hardwoods, Teesdale and MacLean (*25*) concluded that sapwood of all the species was fairly easy to penetrate radially even though the heartwood was resistant. These results are in agreement with the findings of Scarth (*16*) and Weiss (*28*). These qualitative results show the general trend and are the gist of information on lateral penetration. Sutherland, Johnston, and Maass (*23*) in only three comparative runs on seasoned white spruce, found that lateral rate of flow through the sapwood was about 10 times that through the heartwood. Their data are too meager, however, to permit any general conclusions to be drawn.

There is more information on the comparative longitudinal permeability of heartwood and sapwood. Johnston and Maass (*12*) found that longitudinal flow in sapwood of seasoned white spruce and green jack pine was 100 times faster than in the corresponding heartwood. Sutherland and others (*23*) reported that sapwood of three species was from 60 to 10,000 (calculated) times more permeable longitudinally than the corresponding heartwood.

The comparative heartwood and sapwood longitudinal permeabilities were determined directly at low pressure on three species of wood by Erickson, Schmitz, and Gortner (*6*). A wide range of ratios (from 10 to 500 times as permeable in the sapwood as in the heartwood) was found which was determined by the species, the treatment received, and the liquid used. Since the heartwood of the other species tested was not permeable at low pressure, the ratio in those species probably would be very much greater even at higher pressures.

Teesdale (*24*) noted that the color line between sapwood and heartwood of pines did not always coincide with the ease of permeability even in the same cross section of the tree. Scarth (*16*) likewise found

bands or areas of different resistance which extended radially or tangentially in the region of the border line.

The most important structural factor influencing penetration into hardwoods was found by Teesdale and MacLean (*25*) to be the relative absence of tyloses in the vessels. (This is undoubtedly of greatest importance in longitudinal penetration). Next in importance was the permeability of the wood cells to the fluid.

It is not yet clear what role resin canals play in wood permeability and impregnation of woods with fluids. Tiemann (*27*) found that resin canals may or may not permit air to pass through freely. He attributed the difference to the fact that some canals were open whereas others were clogged with resin. Weiss (*28*) explained the difficulty of treating Douglas fir and spruce by the relatively few resin canals which they possess; in southern pines resin canals were more abundant and the woods were easier to treat. Teesdale (*24*) also believed that the resin canal system acted as channels of flow for the preservative fluid. Radial resin canals were believed to be especially effective because when they were present radial penetration was from one-fourth to three-fourths of the longitudinal penetration. The response of one species to treatment could not be applied to another species of similar structure. Inherent differences between species must be recognized.

Weiss (*28*) believed that in Douglas fir heartwood the resin became hard and added to the difficulty of impregnation. Teesdale (*24*) extended this idea of harder and more insoluble resin to include heartwoods in general. He stated that the ease of penetration of the sapwood of pines, spruces, etc., seemed to be a result of the combined effect of the nonresinous structure and the resin canals. The sapwood of species containing canals showed the most erratic absorption, and the most resistant species gave the most uniform results.

In jack pine sapwood, Scarth (*16*) found that resin canals were the chief means of longitudinal penetration, but in the heartwood they were usually blocked by resin or by tylosoids. Johnston and Maass (*12*), after several methods of experimentation, did not deny the effectiveness of resin canals in jack pine heartwood, but their results demonstrated, they believed, that only a part of the flow occurred in this way and that cell penetration did take place under pressure. In attempts to penetrate the wood with safranine solution, they found the dye confined to the first tracheid length and to the resin ducts, but after one-half hour the whole sample was evenly saturated with water, and in spite of the failure of the safranine to move into the tracheids, they believed that this indicated that water moved through the section by means other than the resin ducts. In the opinion of Sutherland and others (*24*), longitudinal flow through sapwood was too rapid to be accounted for by resin canals.

No significant difference in longitudinal rate of flow was found in the areas with or without resin canals in the same part of the annual ring in two southern pine sapwoods investigated by Erickson, Schmitz, and Gortner (*6*).

Most of the available information on directional permeability has been obtained from impregnation studies on wood, although a few measurements of radial and tangential rates of flow have been made. Weiss (*28*) determined the creosote penetration in the three structural directions of several woods by forcing creosote into holes bored into

a wood block of given dimensions and then measuring the distance of penetration. Radial and tangential penetrations were less than the longitudinal penetration; the ratio between them varied with the species.

Teesdale (*24*) found that in woods with resin canals the radial penetration of creosote was from one-fourth to three-fourths of the longitudinal penetration and that the tangential penetration could be disregarded since it was usually a fraction of the radial value. In longleaf pine, for example, the longitudinal, radial, and tangential penetrations were in the ratio of 100 to 4 to 1. In woods without resin canals the radial and tangential penetration were about equal and only one-twentieth to one one-hundredth of that obtained longitudinally.

Johnston and Maass (*12*) reported about the same magnitude of flow in the three directions for jack pine sapwood. In the heartwood, however, longitudinal flow was 100 times that in the two lateral directions. Sutherland and others (*23*) found that in the heartwood of white spruce the apparent penetration radially and tangentially was less than 9 percent of the longitudinal value, although the actual amount penetrating was about 1 percent. In sapwood the radial penetration was less than 2 percent of the longitudinal value. In unseasoned Norway pine sapwood the radial and tangential penetration was less than 1 percent of the longitudinal value. Tangential penetration of white spruce sapwood was somewhat greater than radial penetration. Sutherland and his coworkers admit, however, that these results are not satisfactory largely because of experimental difficulties.

Stamm (*20*) has used radial and tangential permeability to some extent in determining the effect of moisture content on the effective size of the capillaries in the pit membrane and to find the effective size of the capillary openings (*18*).

It is obvious that suitable and extensive data do not exist on directional permeability.

The suggestion is found occasionally in the literature that possibly wood rays aid in the radial movement of liquids in wood. However, relatively few observations have been made and very little study has been done on this specific problem. Teesdale and MacLean (*25*) observed little or no creosote in the wood rays or other parenchyma cells of hardwoods after the preservative treatment. In conifers, likewise, Teesdale (*24*) found that as a rule creosote was not present in wood rays after pressure treatment. In Bailey's (*2*) experiment, carbon particles of the size used did not enter the wood rays. However, Stamm (*18*) pointed out that the effective open capillary structure of tangential sections determined by electroendosmosis corresponded to that of the internal cross-sectional area of the ray cells obtained by microscopic measurements.

It is evident from the above statements that the role of wood rays in the radial permeability of wood is undetermined and that more proof is needed before either view can be accepted. The weight of evidence seemingly favors the idea of impermeability of the wood rays.

There is scattered information in the literature relative to the comparative permeability of springwood and summerwood. In dry loblolly pine sapwood Tiemann (*27*) observed relatively greater permeability in the springwood to air passing in the longitudinal direction by his method of soap films on the surface of the wood.

Weiss (*28*) and Bailey (*1*) observed greater absorption of creosote in the summerwood than in the springwood of longleaf pine. From rather extensive experiments with creosote injection into conifers, Teesdale (*24*) decided that in most woods summerwood was more penetrable than springwood. Redwood, yew, and tamarack were exceptions. Depth of color was used as a basis of comparison. An analysis of one wood, loblolly pine, showed that the summerwood contained 80 percent more creosote than the springwood.

In later work MacLean (*13*, *14*), Teesdale and MacLean (*26*), Griffin (*8*), and Scarth (*16*) found greater penetration and absorption of the preservative fluid in the summerwood by several species of softwoods, principally longleaf pine, Douglas fir, corkbark fir, and spruce. In some species it was often difficult to determine which was the more permeable to zinc chloride (*13*), but with creosote the summerwood was usually penetrated most readily. Scarth and Spier (*17*) forced water-soluble dyes into red spruce sapwood longitudinally and noted quick staining of the springwood but frequently no staining of the summerwood. In the heartwood, contrary results were obtained. Buckman (*4*) found that in the sapwood of freshly creosoted southern yellow pine, the springwood of the majority of the rings contained more creosote than the summerwood. The greater void volume of the springwood afforded a probable explanation. The higher creosote concentration in the summerwood of some rings was attributed to a greater penetration. This occurred only when the total absorption of the ring was low or when conditions of relative free space differed prior to treatment. Buckman pointed out that the data probably could not be justifiably interpreted as meaning a generally greater permeability in the summerwood, although the evidence favored it.

Erickson, Schmitz, and Gortner (*6*) measured the rate of longitudinal flow through the springwood and summerwood of the sapwood of two southern yellow pines to obtain the desired comparison. In both species the springwood was very definitely more permeable to water than the summerwood in both the seasoned and unseasoned specimens. This apparently contradicted most of the preceding work on the problem, but the authors pointed out that the vastly different conditions of the two types of experiments might possibly account to some extent for the disagreement in results on the same woods as reported by others.

Bailey (*2*), after postulating the existence of openings in the pit membrane, explained the great resistance of green woods to flow of air as being due in part to the effect of surface tension in the small openings where numerous membranes had to be traversed. Howald (*10*) could find no constant relationship between the surface tension at an oil-air or an oil-water interface and the penetration of the oil. This does not necessarily exclude the effects of surface tension but probably means that moderately small differences in absolute values for the different oils do not give apparent differences in their penetrance into wood.

According to Scarth (*16*), the sapwood of spruce resisted the penetration of mercury, which stopped at the pits. However, the hindrance was not a structural one, for water flowed through the sapwood and through the pits, as was shown by coloring the liquid. Hawley (*9*) points out that if a liquid does not wet wood the capillary forces

act in the opposite direction of water or against the movement into the capillaries. In such a situation a pressure as high as 50 atmospheres may be required to overcome the capillary forces in the pit membranes and cause intercellular flow. Although equally high capillary pressures may exist in the case of water, Hawley believes that they have little effect in aiding the capillary flow into wood and may actually be retarded by the pit membranes because of the large angle of their surfaces to the mouths of the openings.

Experimental evidence that the presence of air in the wood and that forces of surface tension may affect the rate of flow was obtained by Erickson, Schmitz, and Gortner (*6*). In a heartwood of moderate permeability the rate of flow of water initially and for a short time thereafter was usually less in the unevacuated sections than in the evacuated sections although the final rate of flow was about the same. In the more resistant woods, however, both the initial and the final rates were less in the unevacuated sections than in evacuated sections.

Sutherland, Johnston, and Maass (*23*) determined the effect of surface tension by forcing air through transverse sections of sapwood and heartwood. Difficulty in obtaining flow was encountered only in heartwood sections which had been partly soaked with water. They believed that the Jamin tube effect was responsible for the observed large increase in resistance with increased thickness of the wood section.

APPARATUS AND METHODS

The apparatus and materials used in determining the radial and tangential permeability of woods were essentially the same as those used by the present writers (*6*) in previous investigations on wood permeability.

The apparatus (fig. 1) was constructed entirely of brass in the parts subjected to pressure and of glass and rubber tubing in other parts. The essential features included a brass cylindrical supply tank (*b*) which contained the liquid and was capable of withstanding high pressure. This was connected to a feed line on which were four T connections at regular intervals. To these were attached brass steam valves, and in each was screwed the short length of pipe extending from the center of the lower brass disk. The pair of disks (*c*) was held in alinement by two pegs which fitted into holes in the other disk. The open area through the center of the disks or the area of the sections exposed to the liquid under pressure was 1.47 cm^2. To the top of each upper disk was sealed a glass T tube. On the side was attached rubber tubing and pinchcock and these served as a drain line for the liquid accumulated during the experiment. A burette (*d*) to measure the volume of liquid flow was fastened to the end of the T tube. In the runs in which the rate of flow was not rapid, which was the usual thing, pipettes were used instead of the regular size burette. These pipettes were calibrated to 0.01 cc.

A tank of compressed air (*a*) equipped with a reduction valve was used as a means of producing the desired hydrostatic pressure. The high pressures were read from a gage of 150 pounds per square inch maximum capacity; for low pressure a mercury manometer was employed. The time necessary for a given volume of liquid to flow through the section of wood was timed with a stop watch. In some preliminary determinations, it was found that at high pressure the

sections of some of the less dense woods bulged considerably in the open area exposed to the liquid. A brass retainer was inserted into the opening of the upper disk to serve as a backstop for the section if bulging should occur. This device was essentially a brass tube across one end of which were three raised bars with edges rounded to prevent the wood from being cut. The bars were spaced about 2 mm apart on either side of the center one. By the use of shims on the opposite end, the retainer was adjusted until the bars were only a few tenths of a millimeter beneath the surface of the disk. This seemed to eliminate quite satisfactorily the objectionable bulging and distortion.

No correction for the area of the bars has been made in data reported in this paper, for the following reasons: (1) It could not be definitely determined even on the same section from a number of tests whether

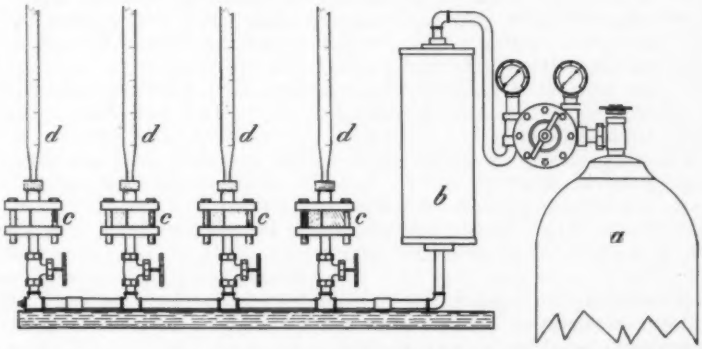

FIGURE 1.—Diagram of the apparatus showing the essential features. See text for description and explanation of lettering.

the retainer really did cause a decrease in rate of flow when the section was pressed against the bars. (2) In the woods tested at low pressure the section would not contact the bars firmly. (3) Not all sections would press against the bars with the same firmness even at high pressure, because the density and rigidity of the woods are variable. (4) It does not necessarily follow that contact with the section decreases appreciably the total flow in the region of the contact.

The initial rate of flow represents the volume of flow in cubic centimeters per minute usually in the first 2 or 3 minutes after the application of pressure. Where the flow of liquid was very slow more time was necessary to make finer adjustments before timing it. In very resistant sections the slight bulging of the section until firmly in contact with the retainer occurred in the first few minutes and might be mistaken for flow of liquid through the section. With some woods the rate of flow was so slow that 5 to 10 minutes was required to obtain a sufficient flow of liquid to permit an accurate measurement.

Most of the determinations were made at a temperature of about 24° C. When the rate of flow was exceedingly small, fluctuations in room temperature were held as constant as possible (within 1°); otherwise expansion and contraction of the liquids in the burettes or of the glass and other parts affected the smoothness of the readings to a noticeable extent.

The rate-of-flow values are nearly always given to three decimal places of significant numbers but not to more than five decimal places. The third digit and the fifth place were not always significant as determined by calculating the effect of probable errors in reading the pipettes and errors of calibration and long timing periods, but for the sake of uniformity these standards were adopted.

The two pressures used in these studies were 10 cm of mercury and 100 pounds per square inch gage reading. The lower pressure was used for those woods that were permeable to the extent of an observed flow of more than 0.002 cc per minute. After the regular 3-hour period of continuous flow, the pressure was increased in some runs to the higher pressure and the rate of flow was measured during a 3-hour period at this pressure. This was done for the woods shown in table 1 except white spruce sapwood, tamarack sapwood, and the sapwoods of loblolly pine and longleaf pine. The 3-hour period was selected as an arbitrary time limit because the rate of flow usually does not change rapidly with time after this period of continuous flow and because it facilitates comparisons on a common time basis. The term "final rate of flow" refers to the rate of flow after 3 hours of continuous flow.

The tangential sections of most species of wood were sawed from freshly felled trees of known history. The radial and tangential sections of eastern hemlock, western hemlock, northern white cedar, Douglas fir (coast type), and white oak were sawed from small seasoned blocks of the same logs used in the study of longitudinal permeability in previous work (*6*). The other radial sections were cut from small seasoned blocks of the same logs from which the tangential sections were sawed. The sections and blocks in the green condition were slowly dried in a cabinet equipped with a fan, two type C Bahnson humidifiers, heating elements, wet- and dry-bulb thermometers, and automatic controls for maintaining humidity and temperature. The temperature in the cabinet was 30° C. The woods were seasoned to about 8-percent moisture content. Sixteen species of wood were used in this investigation. The common and scientific names as given by Sudworth (*22*) are as follows:

Common name	*Scientific name*
"Resinous woods":	
Jack pine	*Pinus banksiana* Lambert.
Loblolly pine	*Pinus taeda* Linnaeus.
Longleaf pine	*Pinus palustris* Miller.
Norway pine	*Pinus resinosa* Solander.
Shortleaf pine	*Pinus echinata* Miller.
Slash pine	*Pinus caribaea* Morlet.
Tamarack	*Larix laricina* (DuRoi) Koch.
White spruce	*Picea glauca* (Moench) Voss.
Douglas fir (coast type)	*Pseudotsuga taxifolia* (Lamarck) Britton.
Black spruce	*Picea mariana* (Miller) Britton, Sterns, and Poggenberg.
"Nonresinous woods":	
Eastern hemlock	*Tsuga canadensis* (Linnaeus) Carrière.
Western hemlock	*Tsuga heterophylla* (Rafinesque) Sargent.
Balsam fir	*Abies balsamea* (Linnaeus) Miller.
Northern white cedar	*Thuja occidentalis* Linnaeus.
Paper birch	*Betula papyrifera* Marshall.
White oak	*Quercus alba* Linnaeus.

In each species the sections used were sawed from at least two different places in the log. Great care was exercised in cutting the

sections so that they would be as nearly perfect as possible. The trueness of the tangential sections to the longitudinal plane was judged by the resin canals and by the annual rings, and in the radial sections by resin canals or vessels when present, but most satisfactorily by examining the sides of the section through a hand lens and observing the deviation, if any, of the cell axis from the plane of the section. The trueness of the sections in the radial and tangential directions was judged by the direction of the wood rays as seen with the aid of a hand lens, and the direction of the annual rings, respectively. If the wood rays, starting near one corner, ran across the section to the other surface before the opposite side of the section was reached, the section was not considered acceptable. In all woods only the best of a number of acceptable sections was used. With some woods good sections were difficult to obtain.

To prevent the liquid that entered the section from flowing eut in a longitudinal direction particularly, but also from flowing out the sides, the ends and sides of the sections were impregnated with paraffin as thoroughly as possible by repeatedly dipping these parts in melted paraffin at from 70° to 75° C. Sudan III was used to color the paraffin, thereby aiding in observing the extent of penetration and capillary rise on the surface of the section while treating. In tangential sections, the resistance of the wood tangentially, which is equal to or greater than that radially, and the greater distance the water would have to move sidewise than through the section, would tend to be effective sealing agents in themselves by acting as hindrances to flow through the sides of the section.

In radial sections the argument of greater distance from the exposed area to the edge of the section also holds, but the resistance of the wood to flow would not be so great. However, in those woods that were very permeable radially, if leaking had occurred it should have been sufficient to be detected by dripping from the disks. No appreciable loss was noticed. The results on several woods, most of which were very resistant tangentially, were checked by applying several coats of a plasticized lacquer to other sections on all but the approximate area of the openings in the disks. The rate of flow or the absence of flow was about the same as in the paraffin-coated sections. Consequently, absence of flow or a very slow rate of flow was not due to leakage from the section. The woods which were checked were tangential sections of longleaf pine heartwood, shortleaf pine sapwood, white spruce heartwood, balsam fir heartwood, Douglas fir sapwood and heartwood, and tangential sections of northern white cedar heartwood. The lacquer method is probably the surest, but it is the most time consuming. The temperature of the paraffin probably caused no permeability changes in the wood, for the air above the liquid was not over 50° C., and the portion of the section not in the liquid would be less than 70° at least. Temperatures below this even on wet wood do not seem to affect permeability permanently (*23*).

All sections were humidified in a desiccator at 90 percent relative humidity prior to coating and also afterward over water for a total of at least 6 hours, and often much longer to prevent checking on the ends when increasing the moisture content after the coating process and before evacuation of the section.

Before each run the sections were evacuated 15 to 20 minutes over water and 10 to 15 minutes in water without breaking the vacuum,

the total time being about 30 minutes. The maximum vacuum drawn over water was 28.5 inches of mercury. The loss in moisture content of the sections during evacuation in air was not large. Some test specimens at 24 percent moisture content lost only 3 percent of moisture during a 20-minute evacuation.

After the evacuation period the sections were allowed to remain under water for 15 minutes or more before they were placed in the apparatus. Care was taken to avoid trapping any air underneath the section during this placement. The sections were so oriented that the retainer bars were at right angles to the longitudinal axis (across the tracheids) in order to maintain the maximum strength properties of the section. The disks were then drawn together, the levels in the burettes were adjusted, and pressure was applied.

Distilled water was used throughout the experiments.

EXPERIMENTAL RESULTS

RADIAL PERMEABILITY AT A PRESSURE OF 10 CM OF MERCURY

Less than one-half of the woods used in this study were appreciably permeable to water radially at a pressure of 10 cm of mercury (table 1). Although a measurable quantity of liquid flowed through these woods none of them showed a high degree of permeability when judged by the ease of liquid flow in the longitudinal direction. This was to be expected because the movement of liquid would be at right angles to the cell axis.

One of the most important facts shown by table 1 is that all the woods except one which were permeable at low pressure were the resinous woods or those which normally possess resin canals longitudinally and radially.[3] With nonresinous conifers an appreciable rate of flow was not obtained during a period of 15 minutes. There may be one exception to this statement, however, and that is balsam fir sapwood. In some determinations the data of which are not reported in table 1, a small rate of flow was obtained at low pressure (10 cm of mercury). These sections were from a different bolt of wood and the treatment of the wood before the sections were cut was not definitely known. Hence the inclusion of the results did not appear advisable. Nevertheless, it may be that some samples of balsam fir sapwood are permeable at low pressure.

Another fact of major importance shown in table 1 is that in almost all cases only the sapwood of the species represented was permeable at low pressure. The springwood of jack pine heartwood was an exception, showing almost the same rate of flow as the sapwood. That this may have been due to chance to some extent is indicated by the greater variation between the individual sections as shown by maximum and minimum final rates of flow in the last two columns of table 1. Some sections of tamarack and Douglas fir heartwoods showed a small rate of flow at low pressure, but many did not; consequently, they were all run only at high pressure.

The more permeable woods were the sapwoods of the southern pines, white spruce, tamarack, and Douglas fir. The variation in the rate-of-flow values for the individual sections of a given wood was of reasonably limited range in most woods. The last two columns

[3] Throughout this paper the term "resinous wood" refers to a wood which possesses a system of resin canals.

give the minimum and the maximum rates of flow at the end of 3 hours of continuous flow.

In general, the rate of flow became less as the time of continuous flow increased. The initial rate of flow was greater than that at any succeeding period except with tamarack sapwood, and the springwood of the sapwood of loblolly pine and white spruce. On an average, the final rate of flow for most woods was about one-third to one-fourth of the initial rate.

It is noticed from table 1 that in several woods the springwood was more permeable radially than the summerwood. The two rates of flow in the southern pines were in the ratio of 4 to 1. This difference is not very great, and the limited sampling reduces the significance of such differences. White spruce, Norway pine, and jack pine were about as permeable in the springwood as in the summerwood at the lower pressure.

TABLE 1.—*Radial rate of flow of water through thin seasoned sections of wood at different pressures*

Kind of wood	Sections	Average thickness	Estimated amount of summerwood	Rate of flow per minute after—					Minimum final flow	Maximum final flow
				0 hours	0.5 hour	1 hour	2 hours	3 hours		
	Number	*Millimeters*	*Percent*	*Cc*	*Cc*	*Cc*	*Cc*	*Cc*	*Cc*	*Cc*
PRESSURE, 10 CM MERCURY										
Jack pine sapwood	4	1.28	0	0.00364	0.00284	0.00228	0.00187	0.00169	0.00118	0.00192
	6	1.20	50	.00920	.00378	.00339	.00223	.00197	.00128	.00345
Jack pine heartwood	5	1.26	0	.02302	.00512	.00360	.00196	.00148	.0000	.0048
Loblolly pine sapwood	4	1.27	0	.0231	.0660	.0555	.0438	.0389	.0205	.0563
	4	1.28	100	.0461	.0217	.0159	.0116	.0095	.0024	.0273
Longleaf pine sapwood	6	1.31	0	.0934	.0590	.0496	.0425	.0388	.0087	.0953
	6	1.29	100	.0260	.0179	.0146	.0146	.0122	.0024	.0273
Norway pine sapwood	4	1.29	0	.00343	.00221	.00169	.00124	.00125	.00070	.00277
	4	1.27	60	.00253	.00154	.00110	.00090	.00082	.00050	.00105
Shortleaf pine sapwood	4	1.29	0	.1315	.0496	.0371	.0303	.0264	.0028	.0482
	4	1.27	100	.03430	.0147	.0109	.0076	.0059	.0031	.0090
Slash pine sapwood	4	1.27	0	.529	.374	.301	.248	.235	.118	.556
	4	1.30	100	.163	.1022	.0791	.060	.0526	.0467	.0545
Tamarack sapwood	7	1.25	30	.381	.648	.548	.418	.354	.182	.588
Black spruce sapwood	5	1.29	0	.0013						
	4	1.26	20	.0010						
White spruce sapwood	8	1.24	0	.1405	.0662	.1514	.0442	.0326	.0092	.0790
	4	1.21	30	.0694	.0430	.0363	.0330	.0304	.0028	.0889
Douglas fir (coast type) sapwood	8	1.29	30	.0650	.0396	.0510	.0296	.0246	.0004	.0861
White oak sapwood	4	1.24	90	.00718	.00569	.00475	.00381	.00319	.00152	.00540
PRESSURE, 100 POUNDS PER SQUARE INCH										
Jackpine sapwood	4	1.28	0	0.812	0.728	0.626	0.511	0.455	0.248	0.556
	5	1.21	50	.949	.574	.607	.488	.415	.179	.724
Jackpine heartwood	5	1.26	0	.959	.407	.301	.215	.181	.0151	.0541
	5	1.25	50	.2704	.0746	.0475	.0271	.0211	.0013	.0381
Loblolly pine sapwood	4	1.29	0	10.86	8.74					
	4	1.31	100	8.66	6.53					
Loblolly pine heartwood	3	1.25	0	1.326	.509	.416	.305	.259	.069	.385
	6	1.26	50	.0417	.0404	.0918	.0860	.0694	.0003	.370
Longleaf pine sapwood	4	1.28	0	7.08	6.19	5.98	5.69	5.49	1.05	13.3
	3	1.29	100	4.77	4.22	3.55	3.01	2.90	1.38	4.79
Longleaf pine heartwood	15	1.27	40	.0246	.0102	.008	.0058	.0046	.0000	.0278
Norway pine sapwood	4	1.29	0	.678	.597	.514	.413	.363	.204	.594
	4	1.29	60	.600	.571	.493	.403	.359	.115	.526
Norway pine heartwood	4	1.31	0	.1528	.0637	.0483	.0249	.0198	.0020	.0392
	5	1.29	40	.0176	.0055	.0046	.0030	.0021	.0000	.0057
Shortleaf pine sapwood	4	1.29	0	15.0						
	4	1.27	100	23.7						
Slash pine sapwood	4	1.27	0	22.4						
	4	1.30	100	18.4						
Tamarack heartwood	15	1.30	0	.656	1.56	1.63	1.70	1.67	.0000	7.52
	18	1.28	70	.414	.518	.544	.497	.442	.0000	2.73

TABLE 1.—*Radial rate of flow of water through thin seasoned sections of wood at different pressures*—Continued

PRESSURE, 100 POUNDS PER SQUARE INCH—Continued

Kind of wood	Sections	Average thickness	Estimated amount of summerwood	Rate of flow per minute after—					Minimum final flow	Maximum final flow
				0 hours	0.5 hour	1 hour	2 hours	3 hours		
	Number	*Millimeters*	*Percent*	*Cc*	*Cc*	*Cc*	*Cc*	*Cc*	*Cc*	*Cc*
Black spruce sapwood	8	1.27	0	.475	1.18	1.15	1.15	1.10	.321	2.50
	8	1.27	20	.570	1.07	1.204	1.38	1.56	.070	4.62
Black spruce heartwood	9	1.30	0	.0037	.0228	.0334	.0421	.0443	.0000	.377
	9	1.27	25	.0033	.0404	.0367	.0095	.0086	.0000	.0267
White spruce sapwood	4	1.21	30	6.43	1.34	1.16	1.47	.689	.235	1.17
White spruce heartwood	9	1.27	0	.190	.202	.191	.174	.163	.0026	.800
	10	1.24	30	.0139	.008	.0053	.0061	.0059	.0000	.0267
Eastern hemlock sapwood	8	1.23	30	.0401	.0199	.0163	.0119	.0101	.0033	.0154
Eastern hemlock heartwood	6	1.23	30	.0021	.0015	.0012	.0009	.0008	.0002	.0015
Western hemlock sapwood	4	1.23	25	.0197	.0090	.0073	.0061	.0056	.0025	.0103
Western hemlock heartwood	5	1.22	20	.0120	.0075	.0059	.0045	.0040	.0004	.0108
Douglas fir (coast type) sapwood	8	1.29	30	5.22	4.67	4.57	4.55	4.50	.072	9.52
Douglas fir (coast type) heartwood	10	1.26	0	.233	.361	.284	.231	.217	.000	.654
	9	1.34	85	.665	.593	.493	.371	.348	.004	.870
Balsam fir sapwood	6	1.24	0	.0366	.0214	.0197	.0185	.0173	.0027	.0289
	6	1.27	35	.0307	.0214	.0195	.0183	.0177	.0089	.0370
Balsam fir heartwood	7	1.27	0	.0031	.0017	.0015	.0013	.0011	.0000	.0025
	6	1.25	30	.0004	.0002	.0002	.0002	.0001	.0000	.0008
Northern white cedar sapwood	7	1.23	20	.0327	.0293	.0278	.0273	.0269	.0013	.0500
Northern white cedar heartwood	11	1.22	25	.0009	.0010	.0010	.0010	.0010	.0000	.0028
Paper birch sapwood	6	1.22	90	.0180	.0105	.009	.0065	.0061	.0040	.0083
Paper birch heartwood	5	1.22	90	0	0	0	0	0	0	0
White oak sapwood	4	1.24	90	.2243	.1305	.0988	.0528	.0407	.0220	.0674
White oak heartwood	4	1.30	100	0	0	0	0	0	0	0

RADIAL PERMEABILITY AT A PRESSURE OF 100 POUNDS PER SQUARE INCH

The data obtained on the radial rate of flow of water through sections of seasoned wood at a relatively high pressure, 100 pounds per square inch are also presented in table 1. These data show great variation in rate of flow among the woods tested. All of the woods except paper birch heartwood and white oak heartwood were permeable at high pressure. Among the most permeable woods were the southern pine sapwoods and Douglas fir sapwood, which had initial rates of flow of from 5 to 30 cc per minute. Those woods that were permeable at low pressure were also the most permeable at high pressure. They include the sapwoods and a few heartwoods of the species with resin canals. A cursory inspection of table 1 will show that for most woods the rate of flow was not of a high order of magnitude, usually only a few tenths of a cubic centimeter or less.

Whenever it was possible, springwood permeability was compared with summerwood permeability. In a number of woods, however, the annual rings were not of sufficient width to permit the cutting of springwood sections of the desired thickness. The sections cut from these woods contained both springwood and summerwood, and in about the same proportions as the original block. The estimated amount of summerwood in the sections containing summerwood is given in table 1. Zero percent designates springwood. Percentages are admittedly not accurate but they represent an estimated average for each series of sections and give some idea of the amounts involved.

Of eight sapwoods tested at high pressure the majority showed about the same permeability in the springwood as in the summerwood. In no case was one part of the annual ring as much as twice as permeable as the other. By species, these sapwoods were: Jack pine, loblolly pine, longleaf pine, Norway pine, shortleaf pine, slash pine, black spruce, and balsam fir. Although the southern pine sapwoods were somewhat more permeable in the springwood at a pressure of 10 cm of mercury this apparently was doubtful at 100 pounds per square inch.

In contrast to this, the springwood of the heartwoods was usually more permeable than the summerwood. The one exception was Douglas fir, which was about as permeable in the springwood as in the summerwood. The springwood of loblolly pine, tamarack, and black spruce heartwoods was 4 or 5 times as permeable as the summerwood; that of jack pine, Norway pine, and balsam fir heartwoods about 10 times as permeable; and that of white spruce nearly 30 times as permeable.

It is desirable when data of this sort are available to make a comparison of the various woods on the basis of their permeability as indicated by rate-of-flow measurements. In so doing two separate arrangements must be made—one including the springwood sections and one including the sections containing summerwood—because the average permeability of some woods was not determined and it may not be a simple average of the springwood and summerwood values or the summerwood values alone. The order of arrangement can be more properly given by dividing the list of woods into groups which are determined in their limits by a shift of one decimal place in relation to the first significant number of the rate-of-flow values.

The order of the woods on the basis of their observed springwood permeability (from table 1) is as follows:

Southern pine sapwoods	1 cc per minute or more.
Tamarack heartwood	
Black spruce sapwood	
Jack pine sapwood	Range, 0.5 to 0.1 cc per minute.
Norway pine sapwood	
Loblolly pine heartwood	
Douglas fir heartwood	
Jack pine heartwood	
White spruce heartwood	
Black spruce heartwood	Range, 0.04 to 0.01 cc per minute.
Norway pine heartwood	
Balsam fir sapwood	
Balsam fir heartwood	0.001 cc per minute.

A similar list based on data from the sections containing summerwood of the amounts indicated in table 1 includes all the species studied. The list in the order of decreasing final rate of flow through the woods is as follows:

Southern pine sapwoods (on basis of initial rate of flow)	1.5 cc per minute or more.
Douglas fir sapwood	
Black spruce sapwood	
White spruce sapwood	Range, 0.7 to 0.3 cc per minute.
Tamarack heartwood	
Jack pine sapwood	
Norway pine sapwood	
Douglas fir heartwood	

Loblolly pine heartwood White oak sapwood Northern white cedar sapwood Jack pine heartwood Balsam fir sapwood Eastern hemlock sapwood	Range, 0.07 to 0.01 cc per minute.
Black spruce heartwood Paper birch sapwood White spruce heartwood Western hemlock sapwood Longleaf pine heartwood Norway pine heartwood	Range, 0.009 to 0.002 cc per minute.
Northern white cedar heartwood Eastern hemlock heartwood Balsam fir heartwood White oak heartwood Paper birch heartwood	Range, 0.0009 to 0.00 cc per minute.

The above classifications are not to be considered as absolute or fixed orders of arrangement but only as an approximate classification in which a wood of one group may belong to another group when different samples or different experimental conditions are employed.

In almost every species the radial permeability of the sapwood was greater than that of the heartwood. In no case was a greater heartwood permeability found, but in two species the heartwood and sapwood permeabilities were not very different; western hemlock sapwood was less than one and one-half times as permeable as heartwood, and the springwood of jack pine sapwood was more than twice as permeable as the springwood of jack pine heartwood. In making such comparisons from the data of table 1, it is obvious that where springwood and summerwood permeabilities were measured separately comparisons of heartwood and sapwood also should be made separately and on the same part of the annual ring.

The approximate ratio of sapwood to heartwood permeability for other species based on springwood, summerwood, or both together is as follows: Jack pine summerwood, 20; Norway pine springwood, 18, summerwood, 170; black spruce springwood, 25, and summerwood, 180; white spruce summerwood, 120; eastern hemlock, 13; western hemlock, 1; Douglas fir summerwood, 13; balsam fir springwood, 16, and summerwood, 130; northern white cedar, 27. Paper birch and white oak heartwoods were practically impermeable so numerical comparison is impossible.

Where comparisons are made on the basis of summerwood sections, it is not meant that the sections were entirely of summerwood; they contained only the amount of summerwood indicated in the fourth column of table 1, which was not always the same for heartwood and sapwood. Considering the small sampling and from only one log, the figures are approximations.

A decrease in rate of flow as the time of continuous flow increased was again the general occurrence, but in this series of tests a number of woods gave increased rates of flow with time as measured by a comparison of initial and final rate of flow. The following woods gave a final rate of flow of water which was from one to three times the initial rate of flow for the same woods: Summerwoods of loblolly pine, tamarack, and northern white cedar heartwoods, and of black spruce heartwood and sapwood and springwoods of tamarack heartwood, black spruce sapwood, and Douglas fir heartwood. In several of these woods, namely, the summerwoods of northern white cedar, tamarack,

and Douglas fir heartwoods, the initial rate was but little different from the final rate of flow. The period of time over which flow continued to increase varied with the kind of wood. The summerwood of black spruce sapwood increased in permeability to water to the very end of the run. In tamarack heartwood the maximum rate of flow was reached after 1 to 2 hours of flow. In other woods, the maximum was reached after ½ to 1 hour.

The sections of a wood did not always behave identically either in increasing or decreasing the rate of flow. Occasionally both processes occurred simultaneously in different sections. The reported values therefore are merely the net result. In some instances the rate of flow fluctuated considerably in the same section during the run. This sometimes occurred in black spruce heartwood and sapwood and in some sections of tamarack and of white spruce sapwood. In several sections of black spruce heartwood the rate of flow increased only slightly during the first 15 minutes or half hour and then suddenly increased very greatly, after which it continued to increase slowly in some of the sections and began to decrease in others. Almost every type of flow situation was found in a few of these resinous woods.

The nonresinous woods did not show these abnormalities in rate of flow. Northern white cedar showed a delayed flow in some sections, but the rate of flow was very small and no striking fluctuations or changes occurred as in the above cases.

Attention should be called to the degree of variation in radial permeability between individual sections of a given wood. Some idea of the variation obtained may be gained by comparing the last three columns of the latter part of table 1, which show the average final rate of flow (after 3 hours), the minimum final rate of flow, and the maximum final rate of flow in the order given. The more resistant woods, in general, show considerable variation. Tamarack heartwood seemed to be the most inconsistent of the group. Some sections cut from the same small piece were very resistant and occasionally showed no rate of flow, whereas a few were very permeable. This was true of the 16 and 18 sections of springwood and summerwood of tamarack heartwood which were tested. In several other woods some sections were apparently impermeable by the methods used. Variations in which the maximum value was 10 times the minimum value were not uncommon, and in a few instances the difference was much greater.

TANGENTIAL PERMEABILITY

The data obtained from experiments on the tangential permeability of the various woods are given in table 2. It is readily seen that the magnitude of the rate of flow is much less on an average than the radial rate of flow (a comparison is presented in table 3). A number of the heartwoods appeared to be impermeable when judged by the technique of this investigation.

The more permeable woods, which generally were the sapwoods, were tested at a pressure of 10 cm of mercury before shifting to the high pressure. A 15-minute period was allowed for the flow of water to manifest itself; if no easily measurable flow (0.005 cc) occurred within that time, the wood was considered to be impermeable by this technique and at this pressure. Only two woods were found through which the flow of water was appreciable—loblolly pine and slash pine sapwoods. Of these two the slash pine was the more permeable and

the average final rate of flow through the sections was 0.003 cc per minute. The rate of flow through loblolly pine sapwood at the end of 1 hour was only 0.0002 cc per minute.

TABLE 2.—*Tangential rate of flow of water through thin sections of seasoned wood at a pressure of 100 pounds per square inch*

Kind of wood	Sections	Average thickness	Estimated amount of summerwood	Rate of flow per minute after—					Minimum final flow	Maximum final flow
				0 hour	0.5 hour	1 hour	2 hours	3 hours		
	Number	*Millimeters*	*Percent*	*Cc*	*Cc*	*Cc*	*Cc*	*Cc*	*Cc*	*Cc*
Jack pine sapwood	4	1.32	25	0.00314	0.00303	0.00326	0.00268	0.00245	0.00154	0.00364
Jack pine heartwood	6	1.26	25	0	0	0	0	0	0	0
Loblolly pine sapwood	3	1.33	60	.0541	.0461	.0408	.0379	.0335	.0286	.0405
Loblolly heartwood	4	1.32	30	0	0	0	0	0	0	0
Longleaf pine sapwood	6	1.34	40	.0375	.0294	.0266	.0221	.0176	.0099	.0357
Longleaf pine heartwood	4	1.32	30	0	0	0	0	0	0	0
Norway pine sapwood	4	1.29	25	.0165	.0124	.0108	.0096	.0086	.0068	.0108
Norway pine heartwood	5	1.28	20	0	0	0	0	0	0	0
Shortleaf pine sapwood	5	1.35	40	.1442	.117	.0969	.0814	.0728	.0287	.1764
Slash pine sapwood	3	1.36	50	.408	.363	.297	.253	.223	.076	.313
Tamarack sapwood	4	1.32	25	.00297	.00273	.00251	.00231	.00215	.00167	.01020
Tamarack heartwood	4	1.32	30	.00199	.00243	.00175	.00159	.00134	.0000	.00323
Black spruce sapwood	4	1.34	15	.00289	.00307	.00289	.00273	.00263	.00204	.00333
Black spruce heartwood	4	1.31	15	.00026	.00012	.00012	.00011	.00010	.00000	.00175
White spruce sapwood	4	1.34	15	.00072	.00158	.00161	.00152	.00150	.00133	.00179
White spruce heartwood	6	1.34	15	.00006	.00008	.00007	.00009	.00011	.0000	.00042
Eastern hemlock sapwood	6	1.31	20	.02753	.01236	.00938	.00638	.00560	.00213	.00923
Eastern hemlock heartwood	4	1.27	20	.00779	.00523	.00405	.00343	.00318	.00090	.00555
Western hemlock sapwood	5	1.27	15	.02531	.00968	.00629	.00440	.00399	.00245	.00545
Western hemlock hardwood	5	1.29	15	.03703	.01980	.01556	.01033	.00838	.00250	.01429
Douglas fir sapwood	7	1.28	30	.00005	.00026	.00075	.00071	.00075	.0000	.00150
Douglas fir heartwood	6	1.30	25	.00040	.00036	.00033	.00036	.00032	.0000	.00106
Balsam fir sapwood	6	1.31	15	.0185	.0139	.0120	.0095	.0081	.0038	.0241
Balsam fir heartwood	8	1.31	15	.00022	.00018	.00017	.00014	.00012	.0000	.00060
Northern white cedar sapwood	4	1.29	10	.0577	.0494	.0478	.0440	.0431	.0397	.0508
Northern white cedar heartwood	4	1.26	10	.0177	.0168	.0162	.0126	.0113	.0024	.0230
Paper birch sapwood	4	1.37	90	.00172	.00253	.00244	.00210	.00201	.00136	.00263
Paper birch heartwood	4	1.31	90	0	0	0	0	0	0	0
White oak sapwood	4	1.37	70	.00876	.00711	.00624	.00583	.00550	.00400	.00796
White oak heartwood	4	1.35	70	0	0	0	0	0	0	0

The phenomenon of decreasing rate of flow with increasing time of continuous flow and a gradual approach to equilibrium was likewise observed in the tangential flow of liquids through wood. In general, the decrease in flow with time was less than was found for radial permeability. For most woods the final rate of flow was from one-half to three-fourths of the initial rate. In four cases the final rate was somewhat greater than the initial rate; these were white spruce sapwood and heartwood, Douglas fir sapwood, and paper birch sapwood. Black spruce sapwood had about the same initial and final rate-of-flow values. The woods in which the final rate was from four-fifths to three-fifths of the initial rate includes jack pine sapwood, tamarack heartwood and sapwood, Douglas fir heartwood, northern white cedar sapwood and heartwood, white oak sapwood, and loblolly pine sapwood. A final rate of flow of about one-half that of the initial flow was found with longleaf pine, shortleaf pine, slash pine, and Norway pine sapwoods, balsam fir heartwood and sapwood. In the remaining woods the final permeability was from about one-third to one-tenth of the initial value. These woods are: Black spruce heartwood,

western hemlock heartwood and sapwood, and eastern hemlock sapwood and heartwood.

These fractional values are not to be regarded as strictly accurate. One reason for this is that much depends upon obtaining the volume of flow during the first few minutes of flow in order that the value may truly represent the initial rate of flow. With woods of very low permeability it was difficult to measure the volume of water coming through the section in only 2 or 3 minutes; hence the period of a measurement was extended to the time necessary to give a fairly accurate volumetric reading. The extra few minutes would tend to change the value somewhat because the reported value would be a near-average of the flow during the total time of the reading during which the rate of flow is usually simultaneously decreasing. This correction also applies for similar cases in radial flow measurements.

A sound reason for caution in any interpretation of a comparison of final and initial rates of flow is that several of the woods increased in permeability during the first 30 minutes or more before the decrease in rate of flow became evident. This group was represented by tamarack heartwood, and the sapwoods of black spruce, white spruce, and paper birch. Douglas fir sapwood and white spruce sapwood were more peculiar in that some sections immediately increased in apparent permeability for a time, then decreased. Other sections did not begin to conduct liquid until 1 or 2 hours had elapsed. They then continued to increase in permeability and thereby offset the declining rate of a few other sections. The result was that the reported data show minor fluctuations or almost constancy over the several intervals of time.

It is not difficult to establish comparisons between heartwood and sapwood permeabilities in the tangential direction. Table 2 shows that in the heartwood of six species either no flow occurred or only an indeterminate amount of water passed through the sections. In these woods, therefore, the moderately permeable sapwood was infinitely more permeable than the heartwood. Such was the case for jack pine, loblolly pine, longleaf pine, Norway pine, paper birch, and white oak. In tamarack, eastern hemlock, and Douglas fir the sapwood was about twice as permeable as the heartwood, in northern white cedar 4 times, in white spruce 15 times, in black spruce 25 times, and in balsam fir 70 times. The one exception was western hemlock, in which the heartwood was twice as permeable as the sapwood. The significance of such a small difference is seriously questioned when the individual variation, shown by the last two columns in table 2, is taken into consideration. This qualification also applies to the three woods in which the sapwood was twice as permeable as the heartwood.

The data in table 2 permit a direct comparison of the tangential permeabilities of the woods. The thickness of the sections is not the same for all woods but is not sufficiently different to affect the results in a general way. The estimated amount of summerwood in the sections is, of course, in the same proportion as in the original piece of wood because of the radial direction of sectioning it.

When the woods are arranged in the order of decreasing permeability and divided into groups the limits of which are arbitrarily fixed

by a shift of one decimal place to the first significant number in the final rate-of-flow values, the list is as follows:

Slash pine sapwood	0.2 cc per minute.
Shortleaf pine sapwood Northern white cedar sapwood Loblolly pine sapwood Longleaf pine sapwood Northern white cedar heartwood	Range, 0.09 to 0.01 cc per minute.
Norway pine sapwood Western hemlock heartwood Balsam fir sapwood Eastern hemlock sapwood White oak sapwood Western hemlock sapwood Eastern hemlock heartwood Black spruce sapwood Jack pine sapwood Tamarack sapwood Paper birch sapwood Tamarack heartwood	Range, 0.009 to 0.001 cc per minute.
Douglas fir sapwood Douglas fir heartwood Balsam fir heartwood White spruce heartwood Black spruce heartwood	Range, 0.0009 to 0.0001 cc per minute.
Jack pine heartwood Loblolly pine heartwood Longleaf pine heartwood Norway pine heartwood Paper birch heartwood White oak heartwood	No apparent flow of water.

The variation between individual sections of a given set of sections was considerably less, on an average, for tangential flow than for radial flow. The last two columns of table 2 show the maximum and minimum final rates of flow for the sections of a given wood. In six woods some sections were apparently impermeable and others of the same wood were somewhat permeable. However, as can be seen from table 2, these sections were not of a high degree of permeability.

In the sapwoods of nine species the maximum values were from about one to three times the minimum rates of flow. This represents a fair degree of uniformity. In three woods the maximum final value was from about 3 to 4 times the minimum; in three woods it was 6 times the minimum, and in one wood it was 10 times the minimum value. Other woods had zero for a minimum. This greater uniformity as compared to the radial flow values was found in both the resinous and nonresinous woods. The woods which exhibited the least variation were: The sapwoods of northern white cedar, paper birch, white oak, jack pine, loblolly pine, Norway pine, black spruce, white spruce, and western hemlock.

In order to determine whether higher pressure would have a deleterious effect on the sections, the pressure was increased to 150 pounds per square inch on several of the woods after the regular 3-hour run at 100 pounds per square inch. In longleaf pine heartwood one section showed a flow of 0.006 cc in 30 minutes and the other three showed no flow. In loblolly pine heartwood only one section showed a very small flow of water and the same was true with four sections of black spruce. In the latter the same section was the only one that permitted flow at both pressures. Two sections each of balsam fir and white spruce heartwoods were tested in the same way. Only

one section of each kind had given a measurable flow at the usual pressure, but at 150 pounds per square inch they increased in rate of flow from one to two times and the other two then revealed a small but definite permeability to water in order of one or two ten-thousandths of a cubic centimeter per minute. This shows that a pressure of 100 pounds per square inch probably did not have a harmful effect on the sections of wood of the thickness used by causing microscopic rupture.

COMPARISON OF RADIAL AND TANGENTIAL PERMEABILITY

The data of tables 1 and 2 afford a basis for comparing in a qualitative way the radial and tangential permeability of a given wood. To enable such a comparison to be made easily, the essential data have been combined in table 3.

TABLE 3.—*Comparison of radial and tangential rates of flow through thin sections of seasoned wood at a pressure of 100 pounds per square inch*

Kind of wood	Radial		Tangential	
	Estimated amount of summerwood	Flow per minute after 3 hours	Estimated amount of summerwood	Flow per minute after 3 hours
	Percent	*Cc*	*Percent*	*Cc*
Jack pine sapwood	0	0.455	25	0.00245
	50	.415		
Jack pine heartwood	0	.181	25	0
	50	.0211		
Loblolly pine sapwood	0	[1] 10.9	60	.0335
	100	[1] 8.66		
Loblolly heartwood	0	.259	30	0
	50	.0694		
Longleaf pine sapwood	0	5.49	40	.0176
	100	2.90		
Longleaf pine heartwood	40	.00458	30	0
Norway pine sapwood	0	.363	25	.00858
	60	.359		
Norway pine heartwood	0	.0198	20	0
	40	.0021		
Shortleaf pine sapwood	0	[1] 15.0	40	.0728
	100	[1] 23.7		
Slash pine sapwood	0	[1] 22.4	50	.223
	100	[1] 18.4		
Tamarack sapwood			25	.00215
Tamarack heartwood	0	1.67		
	70	.442	30	.00134
Black spruce sapwood	0	1.096	15	.00263
	20	1.567		
Black spruce heartwood	0	.0443	15	.00010
	25	.0086		
White spruce sapwood	30	.689	15	.00150
White spruce heartwood	0	.1630	15	.00011
	30	.0059		
Eastern hemlock sapwood	30	.0101	20	.00560
Eastern hemlock heartwood	30	.00077	20	.00318
Western hemlock sapwood	25	.00561	15	.00399
Western hemlock heartwood	20	.0040	15	.00838
Douglas fir (coast type) sapwood	30	4.50	30	.00075
Douglas fir (coast type) heartwood	0	.217	25	.00032
	85	.348		
Balsam fir sapwood	0	.0173	15	.00812
	35	.0177		
Balsam fir heartwood	0	.00109	15	.00012
	30	.00013		
Northern white cedar sapwood	20	.0269	10	.0431
Northern white cedar heartwood	25	.00098	10	.0113
Paper birch sapwood	90	.0061	90	.00201
Paper birch heartwood	90	0	90	0
White oak sapwood	90	.0407	70	.0055
White oak heartwood	100	0	70	0

[1] Initial rate of flow.

In the columns under radial flow, both the final rate-of-flow values of sections containing only springwood and of sections containing summerwood (or springwood and summerwood) are given for the woods in which they were measured separately. The question may arise as to whether the tangential rate of flow should be compared with the springwood value of radial flow for the species or with the summerwood value. The correct answer can only be that the presence of three types of permeability must be recognized: (1) One involving the average of the permeabilities of springwood and summerwood acting independently of each other (in tangential flow); (2) one involving only the springwood radial permeability; and (3) one involving either the summerwood radial permeability alone or the resultant radial permeability of springwood and summerwood acting together in series, depending upon whether or not the section is entirely of summerwood.

In these cases, therefore, tangential rate of flow must be compared separately with the springwood and the summerwood radial rates of flow. With many woods the results will be about the same, for it has already been pointed out that, in the sapwoods, radial rate of flow through the springwood is about the same as that through the summerwood, but in most of the heartwoods this is not true.

Then there is also the fact that where the tangential permeability is compared to the radial permeability of sections containing summerwood, the percentage of summerwood is seldom the same in the two types of sections. One cannot say whether a smaller percentage of summerwood in the radial sections (for tangential flow) than in the tangential sections favors greater tangential permeability, for this depends on the relative permeability of springwood and summerwood in the tangential direction, and on this subject no accurate information is available. It is evident from the above discussion that many comparisons of radial and tangential permeability based on the data of table 3 will at best be only approximations because of the variability of wood, the lack of average values for some woods, the often different amounts of summerwood in the radial and tangential sections, and the possible difference between the average thicknesses of any two sets of sections under consideration. The last item is probably of minor importance as compared with variations in sampling.

Probably the most obvious conclusion from table 3 is the lower average value for tangential flow through the woods as compared to the average radial value determined merely by inspection. Further analysis reveals that this was because of much smaller tangential permeability values for the resinous woods. In fact, several of the heartwoods of the resinous woods were apparently impermeable, thereby exhibiting a sharp contrast to their radial permeability. The resinous sapwoods were also much less permeable tangentially than radially. The nonresinous woods, on the other hand, were about as permeable radially as tangentially on an average.

Aside from those heartwoods which were permeable radially but not tangentially, most of the other resinous woods also showed very decided differences. Jack pine sapwood was nearly 200 times as permeable radially as tangentially, longleaf pine sapwood 160 to 310 times as permeable (based on summerwood and springwood respectively), Norway pine sapwood 40 times, tamarack heartwood 330 to 1,200 times, black spruce sapwood 400 to 600 times, black spruce

heartwood 90 to 440 times, white spruce sapwood 450 times, white spruce heartwood 50 to 1,500 times, Douglas fir sapwood 6,000 times and the heartwood about 1,000 times as permeable.

The differences between the rates of flow in the two directions for the nonresinous woods were not nearly so extreme. Western hemlock heartwood and sapwood, balsam fir sapwood, and the sapwoods of eastern hemlock, paper birch, and northern white cedar were as permeable radially as tangentially or favored either direction by from one to three times. The smaller differences are of doubtful significance. White oak sapwood was about seven times as permeable radially and balsam fir heartwood springwood nine times as permeable radially as the tangentially. The tangential rate of flow through balsam fir heartwood was the same as the radial rate of flow through the summerwood of the heartwood. However, eastern hemlock and northern white cedar heartwoods were respectively 4 and 11 times as permeable tangentially as radially.

Even though these ratios are to be considered as approximations, they very clearly show the marked difference between radial and tangential permeabilities of the woods possessing resin ducts and the relatively small or negligible differences between the two directional permeabilities of the woods without resin ducts.

DISCUSSION

The results of these investigations represent an attempt to establish a number of fundamental relationships of wood permeability which have hitherto been in controversy or have received little or no experimental analysis. In addition, the results have served to verify work which has already been fairly well accepted and at the same time to call attention to cases in which the general rule may not hold true.

There is now little room for doubt that a decrease in permeability with increased time of continuous flow is an almost universal phenomenon in the flow of liquids through wood. The results of this work and that of others (*5*, *6*, *12*, *23*) are evidence for this statement. The number of exceptions to this rule are few. The fact that in some cases an increase in rate of flow is obtained before the decrease begins does not invalidate this conclusion, for it means that other factors are of greater immediate effect and hence outweigh the tendency toward a decrease in rate of flow. The cause of such an increase during the first part of the run is not clearly understood. It was reported in a previous paper (*6*) that surface tension effects were of importance in certain seasoned woods as determined by the effect of evacuation on several heartwoods. All degrees of variation were obtained, depending upon the kind of wood and its resistance to the flow of water. Failure to evacuate the sections sometimes caused the rate of flow to remain the same for a period of time and sometimes resulted in a temporary increase in rate of flow over the initial rate, which was generally lower for the unevacuated sections in such a situation. This was ascribed to the surface tension of liquid in the capillary openings. It seems reasonable to assume that surface tension might have a similar effect on radial and tangential flow. It has been pointed out by Hawley (*9*) that although surface tension forces or capillary pressures of high magnitude may be developed in the small openings of the pit membrane they do not assist materially in the flow of liquid into wood

and may actually retard the rise of liquid in the coarse capillaries of the wood.

Since woods are very resistant radially, and especially tangentially, the effective capillaries must be few or small, or both. In the tangential direction, for example, the liquid must traverse 20 to 40 cells in passing through a section 1 mm thick. If meniscuses must be broken in each encounter with a cell, considerable time may be involved in so doing, for it was noticed with transverse sections that much of the air in a section of a moderately resistant wood was not forced out immediately. In tangential and radial sections evacuation may not be complete in the more resistant woods. If this air were trapped in the cell it would undoubtedly cause a meniscus to be formed at the openings in contact with water and thus block its own outward passage and the flow of water as well. In some situations the water may, because of its high pressure, dissolve considerable of the air and thus free the capillaries.

If a resistant wood is not filled with water by the process of evacuation, and this seemed to be the case in many woods, then some time is necessary for filling the void volume of the section even though it is only about 0.015 cc for the exposed portion of the average section and assuming for the moment that no surface-tension effects occur. The effective void volume is probably greater than this because the liquid would also tend to move into portions of the section other than the area exposed, particularly longitudinally; consequently the given figure might be too small for a resistant wood in which much water has not entered even after evacuation. Where the rate of flow is only of the order of a few ten-thousandths to a few thousandths cubic-centimeters per minute, this is a real situation and seems to apply to tangential flow through very resistant woods.

In radial permeability there is the possibility that, if flow occurs through resin ducts, particles of resin may be torn away and washed out with other loose fragments of resin. This would account for some sudden increases in flow observed in a few sections of white and black spruce.

Without further discussion, therefore, it may safely be said that the increasing rate of flow during the early part of the run that is sometimes noticed in such woods as black spruce and white spruce heartwoods or the long-delayed tangential flow in Douglas fir sapwood, is due to a number of complicating factors which probably are more or less related and often simultaneously effective and which are exceedingly difficult to evaluate.

The results of a comparison of radial and tangential permeabilities of the various woods indicate that radial flow occurs either through the resin canals or through the wood rays.

Microscopic examination of wood shows that the radial walls of tracheids are profusely supplied with bordered pits, the springwood cells having a greater number than the summerwood cells. On the tangential walls, pits are essentially absent in the springwood cells, but are present in most conifers, though usually few, in the last rows of summerwood cells. This may be verified by the literature (*11*).

If flow occurs through bordered pits, a greater rate of flow should be obtained in the tangential direction because of the large number of bordered pits on the radial wall even if a goodly percentage of them were aspirated. The data show, however, that this did not occur.

In fact, the reverse was true, for the woods with resin canals. There is a possibility that the water may follow a roundabout course in moving radially through the section by taking advantage of the unsymmetrical arrangement of cells which usually exists to some extent in springwood. In this case the water would pass through the radial wall into the lumen of an adjacent cell and out through the other side of the same radial wall into a third cell which, with the first cell, has part of its radial wall in contact with the second cell, somewhat in the fashion that bricks are laid. This is a possible mechanism because most of the woods have a double row of pits either rarely or frequently, and in such a situation are likely to have pits on the same wall leading to two different cells.

While this mechanism may be a possibility in the springwood, it is very unlikely in the summerwood because of the more regular and linear order of the cells tangentially, the narrower width radially, and fewer pits. Although pits are present in the tangential walls of the last few rows of summerwood of conifers, except in the hard pines, they probably do not assist in radial flow because there is no apparent way by which the liquid could traverse the entire summerwood or pass beyond into springwood cells. Then, too, the results are about the same for woods with or without tangential pits. Further proof that these pits must be of minor importance, if any, lies in the fact that in both jack pine sapwood, a resinous wood, and balsam fir sapwood, a nonresinous wood, the springwood and summerwood of each wood were equally permeable. If the zigzag or roundabout path of flow were of importance, springwood permeability should have been much greater than that of summerwood. Furthermore, tangential permeability should have been greater than radial permeability because of the greater number of openings, and the more direct path of flow. Only relatively few cells are appropriately arranged for liquid movement through the bordered pits in a radial direction.

It has already been stated that the radial permeability of the nonresinous woods was not very different on an average from the tangential permeability. Thus it appears from the above discussion that the liquid must flow through the wood rays in a radial direction and through the bordered pits of the radial walls in tangential movement.

The two most probable paths of radial flow in the resinous woods are woodrays and resin canals. The fact that the radial flow through these woods was much greater than the tangential flow, which was usually not true of the nonresinous woods, suggests that the added structural feature in the radial direction was chiefly responsible, namely, the resin canals. It is true that some of the species, the pines in particular, have more ray tracheids than the nonresinous woods (*3*), but the other species of both groups tend to discredit the importance of these structural features. For example, black spruce, white spruce, and Douglas fir all have only one row of marginal ray tracheids, yet these woods show great differences between radial and tangential permeabilities. Eastern hemlock and western hemlock also have one row of marginal ray tracheids and show little difference between their radial and tangential permeabilities. The radial rates of flow for the sapwoods of the above species both with and without resin canals are not even approximately the same, and they should be so if the amount of ray tracheid tissue were the important factor, even though allow-

ance is made for a variation of 100 percent in the total wood-ray cross-sectional area.

It is interesting to note, however, that there was a certain uniformity or agreement in values for radial permeability of the nonresinous sapwoods and the sapwoods of white oak and paper birch. The values read as follows in cubic centimeters per minute: 0.01, 0.006, 0.017, 0.006, 0.027, and 0.04. The two lowest values belong to western hemlock and paper birch sapwoods. The tangential permeability of paper birch and white oak sapwood was one-third and one-seventh, respectively, of the radial values.

Returning to a consideration of radial flow in the resinous woods, it is believed that the explanation offered by other workers best fits the experimental data. Tiemann (*27*) suggested that in the sapwood the resin canals may be open or clogged; Weiss (*28*) and Teesdale (*24*) attributed the greater resistance of the heartwoods to creosote impregnation to the harder and more insoluble resin in the resin canals of the heartwood which would close up the canals more effectively. This would explain the large sapwood permeability as compared with that of heartwood. The presence of tylosoids in the resin canals of the heartwood of some species (Norway pine, jack pine, and the four southern pines) would also hinder liquid flow through the canals if one assumes that they are effective in the conduction of liquid.

The peculiar variations in rate of flow of some resinous woods, as noted in the experimental results, is most easily explained on the basis of the effectiveness of the resin canals. Sudden increases in rate of flow might be due to the forcing out of particles of resin adhering to or clogging the canal. On the other hand, some particles might be broken loose but encounter larger particles and cause a jam with cumulative effects unless it were weakened in some way and flushed out. From the variations in rate of flow obtained in some woods, notably white spruce, black spruce, tamarack, and Douglas fir, this is a possible explanation. For one section of white spruce sapwood summerwood the rate of flow after 15 minutes was only 13 percent of the initial flow. At 1.5 hours the flow was 80 percent greater than at 1 hour, and after 2.5 hours the flow was again the same as at 1.5 hours. Sections of Douglas fir heartwood cut from the same piece were often very different in rate of flow, some showed only a slight permeability initially and stopped altogether after 0.5 to 1 hour, and others showed rates of flow a few tenths of a cubic centimeter or more.

It is an interesting fact that these woods which showed abnormal rate-of-flow curves at high pressure did not do so at 10 cm of mercury (table 1). High pressure seemed to bring out more variation and discrepancies within the same section or between sections of the same kind of wood.

Although the phenomenon of an increase in rate of flow preceding the usual decrease with time was found in tangential flow, it was always of a smaller or negligible magnitude, more regular, taken section for section, and less frequent by species than in radial flow.

If difference in rate-of-flow curves for the different sections is attributed to surface-tension effects of a water-air system in the wood, then the greater and more sudden variations in flow in radial direction as compared to the tangential direction again indicate that the capillaries are larger radially when freed from hindrances to flow of water, and are more easily opened up than the tangential capillaries, which

also should mean a larger and more direct capillary. Again, this points to resin canals because the flow through resinous woods radially was usually much greater than tangentially and greater also than radial flow through nonresinous woods.

The discussion so far has not taken into account the possible permeability of the cell wall itself, exclusive of the pit membranes. Considering the nature of the cell wall, its submicroscopic and microscopic structure, and the fact that the cell-wall substance in the direction across the fiber becomes of considerable thickness even in a thin section, it does not seem likely that cell-wall permeability is important in these experiments. A number of woods showed no apparent flow of water by the methods used. This is evidence that the cell wall itself was practically ineffective in conducting water as measured by this technique. Stamm (*21*) from calculations of his data found that the pit-membrane pores were far more important as a cause of permeability to flow under pressure in the three structural directions than cell-wall permeability. The latter was negligible by comparison except in extremely resistant woods.

The idea that resin canals function in the flow of liquid in wood is not a new one. A comprehensive review on this topic has been given in the review of literature. From this scattered and somewhat contradictory information it is concluded that with different conditions, woods, and direction of flow, the resin ducts may or may not function. The results of creosote impregnation tests at high temperature may be different than when water, lower temperature, and thin sections are used; nor may the results obtained longitudinally be always applicable to radial penetration. At any rate there is evidence in the literature that resin canals may transport liquid radially, although there is no proof that they are the sole means of radial movement. In this paper the possible mechanism of radial flow has been developed from more complete data than have hitherto been available and without the support of other experimental work, although it is seen that several of the ideas are in agreement.

The disturbing feature to the suggestion that wood rays are effective in radial flow lies in the counter reports in the literature. Teesdale and MacLean (*24*, *25*) found little or no creosote in the wood rays or other wood parenchyma of both hardwoods and softwoods. Bailey observed no entrance of carbon particles into the wood rays of several conifers (*2*). Stamm (*18*), however, noted that the effective area of tangential sections of several woods was about the same as that of the ray cells, but this can only be considered as indirect evidence of wood-ray permeability. In a later paper MacLean (*14*) states that "little is known about their influence on penetration," but that in some hardwoods whose vessels are plugged by tyloses the simple pits (of wood rays and other parenchyma) may aid in penetration.

Some qualitative evidence that the wood-ray cells are permeable was obtained by examining the tangential sections of southern pine near the edges where they were sealed with paraffin. Under low-power magnification the colored paraffin was seen in the wood rays apparently in some rows of cells and not in others. A detailed examination was not possible, but the observation warrants further investigation into the problem of wood-ray penetrability.

Concerning the relative penetrability in three structural directions, penetration is considered to be greatest longitudinally, and radial or

tangential precedence is variable. The radial penetration is reported by MacLean (*14*) to be greater in some pines, but the tangential penetration in most of the other conifers is usually greater except in some resistant species where the difference is small. In the present series of experiments, tangential permeability greater than or equal to the radial permeability was unusual in resinous woods, but the contrary was fairly common in the nonresinous woods.

The results of investigations on creosote impregnation of wood by Weiss (*28*) and Teesdale (*24*) agree fairly well in a qualitative way with the results reported in this paper on the comparison of radial and tangential permeabilities. In resinous woods they found greater penetration of creosote radially than tangentially and in nonresinous woods the penetrations were about equal. Sutherland, Johnston, and Maass (*23*) found about equal permeability radially and tangentially in seasoned white spruce sapwood. In this work, however, the radial flow was over 400 times the tangential flow. The statement by Johnston and Maass (*12*) that jack pine sapwood is of the same order of permeability in the three structural directions is undoubtedly in error. Their conclusions were based on only one test in each direction.

Several exploratory experiments by Sutherland, Johnston, and Maass (*23*) indicated that in the two species tested the radial and tangential rates of flow were from 2 percent to less than 1 percent of the longitudinal rate of flow. Creosote penetration measurements (*24*, *28*) are of the order of 10 to 100 times greater penetration longitudinally than tangentially, with the radial comparison ratio usually somewhat less.

Comparisons of the rate of flow in the three structural directions were not determined directly in the present series of investigations. However, a rough idea of the relationships may be obtained if certain assumptions are made. Data on longitudinal permeability of the same species used in this study were obtained in previous studies by the present writers (*6*). By comparing those values with the values obtained in this work approximation of ratios may be arrived at. The transverse sections were 1 cm. The effective thickness, however, in sections only a few tracheid lengths in thickness, would be less than this if it is assumed for all woods that flow is chiefly through the pit membranes in transverse sections, because the liquid would pass through one-fourth of an open fiber length at each end, on an average (*20*). The number of cell walls traversed would therefore be the actual thickness minus one-half the average fiber length. The average length of jack pine tracheids is about 3.5 mm, depending on the age of the tree and the height. The effective thickness was therefore about 8.3 mm. Let it be assumed that this is the approximate value for the other species also. The effective thickness of the radial and tangential sections is essentially the same as the measured thickness because of the large number of cells and their small diameters. The average thickness for the radial and tangential sections was between 1.25 mm and 1.3 mm. Thus the effective transverse section is about 6.4 times as thick, and this correction must be applied. In doing so it is assumed that the rate of flow varies in inverse proportion to thickness of the section, which does not seem to be strictly true (*23*), but no correction factor is available. The high pressure used in lateral permeability tests was 5 times and 103 times that used for

transverse sections, depending on the kind of wood. In calculating to a common pressure basis, 100 pounds per square inch, a direct proportionality is assumed between rate of flow and applied pressure, which is not always the case. However, in white spruce heartwood and sapwood, black spruce heartwood, and Norway pine sapwood it has been observed that longitudinal rate of flow increased in direct proportion to the pressure applied (*4*, *23*). Hence, the pressure correction factor should be eliminated in comparisons on these woods.

On a basis of rate of flow through sections 1 cm thick and at a pressure of 100 pounds per square inch, the relationships in directional permeability of the aforementioned woods are as follows: In white spruce sapwood (all woods referred to were seasoned) the longitudinal permeability was about 70 times the radial permeability and 30,000 times that tangentially; white spruce heartwood was 850 times more permeable longitudinally than radially and 50,000 times more permeable longitudinally than tangentially. In Norway pine sapwood, longitudinal permeability was 2,000 times the radial value and 90,000 times the tangential value. In black spruce heartwood, longitudinal permeability was 110 times the radial permeability and 9,000 times the tangential permeability. In white spruce heartwood, Sutherland, Johnston, and Maass (*23*, *table VII*) have shown practically an inverse proportionality between longitudinal rate of flow and thickness for sections varying about 250 percent in thickness. If the same may be assumed for increases in radial and tangential thickness, then the values for white spruce heartwood should be valid.

Buckman, Schmitz, and Gortner (*5*) found a disproportionately greater rate of flow with increased pressure in eastern hemlock heartwood. Their data when plotted to a smooth curve show that the rate of flow at 100 pounds per square inch was about five times greater than would be expected if a linear relationship existed with the origin and the flow value at 20 pounds per square inch as the determining points for extrapolation. If this is assumed as a rough means of determining the correction to be applied, then approximations on eastern hemlock directional permeability may be made. The longitudinal permeability thus corrected was about 42,000 times the radial permeability and 10,000 times the tangential permeability.

In the above comparisons, if the longitudinal flow of liquid is assumed to go through the resin canals, where present, then the effective thickness of the transverse section is the same as the actual thickness (1 cm) and the longitudinal values of the ratios are increased by about 12 percent. A second consideration is that even if flow decreases faster with increasing thickness of the section than in simple proportion, then in adjusting for thickness of thin radial and tangential sections to a common basis, 1 cm for example, the corresponding flow values would also be decreased in disproportion and when comparisons are made to longitudinal flow, the directional permeability ratios would be even greater than those reported above.

Somewhat the same argument applies to the pressure adjustments from low to high pressure. The rate-of-flow values obtained at lower pressures and extrapolated linearly to high pressure should be minimum values because actually the rate of flow may be greater than a linear function of pressure, which would result in higher values than those obtained by extrapolation. This would result in greater differences between longitudinal and lateral rates of flow values.

The date of Buckman, Schmitz, and Gortner (*5*) permit the elimination of the pressure variable with a few woods. In certain of their experiments on longitudinal rate of flow, woods were run to equilibrium at a pressure of 100 pounds per square inch. This permits direct comparison from the pressure standpoint and leaves only the possible error in adjusting for greater thickness of sections which is not included in the comparative results. The thickness of the transverse sections in their experiments was from 1.1 to 1.35 cm. The smaller area exposed to the path of flow in their apparatus was corrected for in the rate-of-flow values used for the comparisons to be given.

For the five woods which they used and which were also used in this investigation, the directional permeability comparisons are in reasonably good agreement considering the fact that different samples of wood were used and that the conditions of the experiment were not exactly the same. In the case of balsam fir heartwood the ratios are greater when the observed rate of flow is used than when the value calculated from the rate of flow at 20 pounds per square inch is used and assuming a proportional change in computing the flow at 100 pounds pressure. The same was true with eastern hemlock heartwood. This undoubtedly was due chiefly to the disproportionate increase in rate of flow with increase of pressure. The flow was measured at the desired pressure in the one case and in the other it was computed linearly from a value which was actually on a curve instead of on a straight line. For Norway pine sapwood and white spruce sapwood, however, the use of a linear relationship in computing the flow at high pressure gives fair agreement with their observed values for longitudinal flow. This also confirms reports that in these woods the rate of flow varies in direct proportion to the pressure.

The ratio of longitudinal to radial to tangential permeability is given in table 4 for a number of woods. In certain of these ratios the longitudinal value was calculated by using the data of Buckman, Schmitz, and Gortner (*5*), the rate-of-flow values of which were obtained at 100 pounds per square inch. In the other ratios the longitudinal value was calculated from the data of Erickson, Schmitz, and Gortner (*6*) which was computed by direct proportion to the basis of 100 pounds per square inch. In both methods a simple inverse ratio between permeability and thickness of the section has, of necessity, been assumed.

In table 4 if the radial permeability of springwood and summerwood were measured separately the smaller value was used for comparison. The ratios given are only approximations in round numbers. In most instances the ratios for the sapwoods are considerably greater than those for the heartwoods except in those woods that decrease in permeability from seasoning. The effective thickness of the transverse sections of conifers was considered to be the actual thickness minus 0.17 cm for the sake of uniformity and because it is not definitely known whether longitudinal flow induced by pressure occurs chiefly through resin canals when they are present. In the two hardwoods the actual thickness was used. For reasons pointed out previously, some of the longitudinal values of the ratios are probably too small.

TABLE 4.—*Ratio of longitudinal to radial to tangential permeability for woods of several species*

Kind of wood	Ratio of directional permeabilities			Kind of wood	Ratio of directional permeabilities		
	Longitudinal	Radial	Tangential		Longitudinal	Radial	Tangential
Norway pine sapwood	90,000	40	1	Jack pine sapwood	400,000	150	1
Do	[1] 70,000	40	1	Jack pine heartwood	5	1	0
Norway pine heartwood	50,000	1	0	Longleaf pine sapwood	100,000	150	1
Balsam fir sapwood	200,000	2	1	Longleaf pine heartwood	9,000	1	0
Balsam fir heartwood	120,000	1	1	Black spruce heartwood	10,000	90	1
Do	[1] 900,000	1	1	Western hemlock sapwood	600,000	1	4
Northern white cedar sapwood	10,000	1	2	Western hemlock heartwood	7,000	1	2
Northern white cedar heartwood	60,000	1	10	Slash pine sapwood (based on initial flow)	30,000	45	1
Do	[1] 60,000	1	10	Douglas fir (coast type) sapwood	1×10^7	6,000	1
Eastern hemlock sapwood	100,000	2	1	Douglas fir (coast type) heartwood	50,000	700	1
Eastern hemlock heartwood	9,000	1	4	Paper birch sapwood	1.7×10^6	3	1
Do	[1] 150,000	1	4	White oak sapwood	35,000	7	1
White spruce sapwood	30,000	45	1				
Do	[1] 20,000	45	1				
White spruce heartwood	50,000	60	1				

[1] Longitudinal value of ratio calculated by using data of Buckman, Schmitz, and Gortner (*5*), rate-of-flow values of which were obtained at 100 pounds per square inch.

Because of the variety of conditions under which other data have been obtained, namely, different thicknesses of test specimens, different pressures, pretreatments, temperatures, liquids, and time, it seems futile to attempt critical and detailed comparisons of springwood and summerwood permeabilities and of heartwood and sapwood permeabilities. The conclusion that in most conifers summerwood is more permeable than springwood (whether longitudinal, radial, or tangential is often not specified) is shared by Weiss (*28*), Teesdale (*24*), Scarth (*16*), MacLean (*14*), Bailey (*1*), and Griffin (*7*, *8*) from their investigations on one or more woods. This generalization does not find much support from the data of these experiments on radial permeability. The results of Buckman's experiments (*4*) on creosote distribution in southern pine sapwood appear to be in somewhat better agreement with these data than do those of the above-mentioned experiments. The considerably greater longitudinal permeability of the springwood as compared to the summerwood as found by Erickson, Schmitz, and Gortner (*6*) in two southern pine sapwoods does not seem to hold true in the radial direction. Radially, there was little difference in rate of flow between springwood and summerwood of the southern pine sapwoods. The direction of flow, therefore, appears to affect the relationship of springwood and summerwood permeability.

No information was obtained, by the technique employed, on the relative permeability of springwood and summerwood in the tangential direction. It would seem that there must be radial movement for penetration but that ease of tangential flow would insure better distribution of the fluid if the radial movement tended to be erratic or localized.

The greater radial permeability of the sapwood as compared to that of the heartwood in the resinous woods is in accordance with the results of investigations by Weiss (*28*) and Teesdale (*24*) on creosote penetration. Teesdale found no difference in absorption or penetration between the heartwood and sapwood of eastern and western hem-

lock. In this investigation western hemlock was about as permeable (radially) in the heartwood as in the sapwood, but the heartwoods of eastern hemlock, balsam fir, and northern white cedar were from less than one-tenth to less than one-thousandth as permeable as the corresponding sapwoods. The low value for northern white cedar heartwood may be explained on the basis of the infiltrated substances but there seems to be no satisfactory explanation of the differences in the other species unless it is that the process of heartwood formation affects the permeability of some species more than others.

The sapwoods of white oak and paper birch were both permeable at high pressure. Teesdale and MacLean (*25*) also report that the sapwoods of hardwoods are fairly amenable to preservative treatment even in species in which the heartwood is difficult to treat. White oak is one of this group. Though the ease of preservative treatment may be due somewhat to the open vessels in the sapwood of the hardwoods, this cannot be the case in these investigations because of the method of preparing the sections; hence, the flow obtained was truly radial flow.

During the investigations with black spruce, white spruce, and balsam fir erratic results were occasionally obtained when sections cut from near the border line of heartwood and sapwood were used in permeability tests. A section which was sapwood according to the moisture line gave about the same permeability as the heartwood sections of the same species. The same situation was sometimes true for heartwood sections cut within several rings of the border line as determined by the moisture content in the green wood The border-line zone was therefore avoided in cutting out sections for permeability tests in all species.

It is fully realized that imperfections in the sections, either due to inherent defects in the wood or to improper sawing of the section, would influence the results to a greater or lesser extent. Only wood free from defects such as small knots, compression wood, traumatic canals, etc., was used. In a few woods the grain was so irregular and wavy or the wood rays so curving that perfect sections were practically impossible to obtain from the blocks. This trouble was encountered more often with the radial than with the tangential sections. However, so far as could be discerned by comparisons with other sections, the error involved is not serious, particularly from a qualitative standpoint. It is not denied, however, that it may have made the difference between a measurable flow and no flow at all in a few sections in several woods whose radial permeability was very much greater than their tangential permeability as, for example, Douglas fir.

On an average, there was less variation between sections in tangential flow than in sections on which radial flow was measured. This may be explained thus: In radial flow only a fraction of a ring to several rings, depending on the width of the annual rings, is measured in any one section. Usually it was one ring or less. Hence, the permeability of four annual rings, let us say, would be measured separately. In tangential flow, however, several rings are included in a section because the plane of the section is at right angles to the rings. The flow obtained, therefore, would be the combined flow through several rings. Hence a more average value would be expected than in the case of radial flow. This consideration is exclusive

of the effect that resin canals in resinous woods may have on permeability.

The thickness of the sections for the same or for different species was not always the same but in most sections did not go outside the limits of 1.2 to 1.35 mm and was usually near the average of these limits. No consistent correlation of rate of flow with small differences in thickness was evident. A test run on a set of tangential sections of birch sapwood (which normally seemed to be quite uniform in permeability) of different thicknesses showed that differences of about one-fourth did not make a serious difference in flow in such a small sample. It may be assumed, therefore, that the errors due to differences in thickness of the sections are less than the variations due to sampling even in the same piece of wood.

SUMMARY AND CONCLUSIONS

The radial and tangential permeability to water of 16 species of wood in the seasoned state have been determined. Heartwood, sapwood, springwood, and summerwood were studied when conditions permitted it. Most of the sections were 1.25 to 1.30 mm thick.

Most of the sapwoods of the resinous species were appreciably permeable radially at a pressure of 10 cm of mercury. In general, this was not true of the nonresinous woods.

Nearly all woods, whether heartwood or sapwood, were permeable radially at 100 pounds per square inch. The resinous sapwoods were much more permeable and showed greater variation than the nonresinous sapwoods.

Sapwood was more permeable radially than the heartwood of the same species, except in rare cases. The range of their ratios was very wide.

Summerwood was almost as permeable as springwood in the radial direction at high pressure in the sapwood of the species tested in this way. In the heartwood, springwood permeability was usually greater.

The woods have been grouped on the basis of their magnitude of radial permeability to water at high pressure. A similar arrangement has been made on the basis of tangential permeability of the woods.

The tangential permeability of resinous woods both in the heartwood and in the sapwood was very much less than the radial permeability.

Some heartwoods, including four pines and two hardwoods, were practically impermeable tangentially when judged by the methods employed.

The differences between radial and tangential permeability in nonresinous woods were usually small or of questionable significance.

Several species were about as permeable tangentially in the heartwood as in the sapwood. Other species were definitely more permeable in the sapwood and to a varying degree.

From a consideration of the experimental data and the structural features of wood, the radial flow through the sections of resinous sapwood apparently was chiefly through the resin canals. Radial flow through the resinous heartwood sections may have been assisted by the resin canals or the wood rays, or both.

The uniformity of radial rates of flow of the nonresinous sapwoods, their lower values as compared to the resinous sapwoods, and other considerations suggest that the wood rays are important paths of

radial flow in these sapwoods. Among the heartwoods, the permeabilities were very different, probably due to differences in the transition to heartwood.

In general, the rate of flow decreased with increasing time of continuous flow and approached equilibrium. In some cases a short period of increasing rate of flow preceded the decrease. In rare instances the rate of flow increased somewhat even in the later periods of flow.

Factors such as the surface tension in the capillaries, the void volume of the section, the presence of air in the wood, and the condition of the resin canals may have been responsible singly or collectively for some of the observed variations in flow.

The ratios of the permeabilities in the three structural directions are given for a number of woods. When rate-of-flow values were calculated to a standard basis, longitudinal permeability was usually thousands of times greater than lateral permeability.

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A STREAK DISEASE OF PEAS AND ITS RELATION TO SEVERAL STRAINS OF ALFALFA MOSAIC VIRUS [1]

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INTRODUCTION

A virus disease of peas (*Pisum sativum* L.), manifested by a streaking of the stems and leaves and a spotting of the pods, was observed under greenhouse conditions at the Arlington Experiment Farm, Arlington, Va., in the fall and winter of 1934. The disease in general resembles the streak disease described by Linford,[3] in 1929, as occurring in pea fields throughout the United States, and the spotted wilt of peas recently described by Whipple (*17*).[4] The viruses of alfalfa mosaic likewise produce on peas and other hosts, symptoms that are somewhat similar to those produced by the pea streak virus. In the early stages of these investigations it was reported by Zaumeyer and Wade (*21*) that the pea streak disease was caused by an alfalfa mosaic virus. This assumption was based on the similarity of symptoms produced by the pea streak virus and the alfalfa mosaic viruses on a number of hosts. Since that time it has been proved by Zaumeyer (*18*) that the pea streak virus is different from the alfalfa viruses reported here. It is likely, however, that these viruses may be related. This paper reports the results of a study of three strains of the alfalfa mosaic virus in comparison with the pea streak virus. Data are also presented on the differentiation and identification of these viruses.

HISTORY

The origin of the pea streak disease herein reported is not definitely known. In a proposed study of resistance and susceptibility of peas to a virus of red clover (*Trifolium pratense* L.), a number of pea varieties were planted in greenhouse benches. Windsor broadbeans (*Vicia faba* L.) were planted every fifth row and later were inoculated with a virus from red clover collected at Arlington. After the mosaic symptoms appeared on *V. faba*, large numbers of the pea aphid, *Illinoia pisi* (Kalt.), which had been reared on healthy *V. faba* plants for several weeks in cages, were released in the greenhouse by being placed on *V. faba* plants that were growing in the greenhouse benches and were infected with the red clover mosaic virus. The aphids later migrated or were artificially transferred to the peas growing in adjacent rows. The pea aphids used were originally collected from apparently healthy alfalfa plants growing in the field near Arlington.

About 3 weeks after the release of the aphids, spots resembling

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[2] The writer expresses his appreciation to L. L. Harter and B. L. Wade, of the Division of Fruit and Vegetable Crops and Diseases, for helpful advice given during the course of the investigation.

[3] LINFORD, MAURICE B. PEA DISEASES IN THE UNITED STATES IN 1928. U. S. Bur. Plant Indus., Plant Disease Reptr. Sup. 67, 14 pp. 1929. [Mimeographed.]

[4] Reference is made by number (italic) to Literature Cited, p. 771.

those produced by *Alternaria* sp. appeared on the leaves of the *Vicia faba* plants. Microscopic and cultural studies proved that these lesions were not produced by fungi or bacteria. These spots were followed by a streaking of the stems and petioles, defoliation, and finally by the death of many plants. Somewhat similar symptoms appeared on the peas, and within a short period the disease became widespread throughout the peas and Windsor broadbeans growing in the greenhouse.

After inoculation with the virus from red clover and before release of the aphids to them, only the typical mottling appeared on the inoculated *Vicia faba* plants. Since the streak disease first appeared on the *V. faba* plants about 3 weeks after the release of the aphids, it was assumed that the virus may have originated from infective aphids. Freezing outdoor temperatures at that time made it impossible to determine whether the alfalfa plants where the aphids were collected were the source of the disease. In the spring of 1935, however, it was found that a high percentage of the alfalfa plants in the field were infected with mosaic.

Collections of mosaic-infected alfalfa plants were made both at Arlington, Va., and in Colorado. Inoculations with the viruses of the mosaic-infected plants showed that two viruses were present in the material from Virginia and that both were different from the virus collected in Colorado. The three viruses, when inoculated to *Vicia faba*, produced symptoms somewhat similar to the pea streak virus. On peas the symptoms of one of the alfalfa viruses showed marked similarities to the pea streak virus.

Notwithstanding this similarity in symptoms, the pea streak virus differs distinctly from the alfalfa viruses. Since it has been impossible to isolate the pea streak virus from later collections of mosaic-infected clover material, it is believed that the virus may have originated from infected alfalfa plants and may have been transmitted to peas and Windsor broadbeans by the pea aphid.

EARLIER INVESTIGATIONS

Linford,[5] in 1928, described a streak disease of peas that he found in pea fields from the Atlantic coast west to Utah and Montana. He (*5*) later found that *Thrips tabaci* Lind., if transferred to peas after having fed on infected *Emilia sagittata* (Vahl) DC., produced symptoms identical with the earlier recorded pea streak. Likewise thrips reared on infected pea plants transmitted the disease to peas as well as to pineapple, producing the typical yellow spot disease.

Weimer (*15, 16*) reported on the transmissibility of an alfalfa mosaic but recorded no cross-inoculation studies. Zaumeyer and Wade (*19, 20*) showed that the alfalfa virus of Weimer, as well as an alfalfa virus collected in Virginia, was infectious to beans and other legumes. Pierce (*8*) also described an alfalfa mosaic that was infectious to bean, pea, *Vicia faba*, and other leguminous hosts.

Zaumeyer and Wade (*19, 22*) and later Pierce (*7*) showed that the viruses of sweetclover and white clover cause streak symptoms on pea.

Pierce (*7*) also reported a broadbean local-lesion virus that produced streak symptoms on peas, especially when in combination with other viruses. The relation of this virus to Linford's pea streak virus was not shown.

[5] LINFORD, MAURICE B. See footnote 3.

Whipple (*17*) recently reported a pea streak as being caused by the spotted wilt virus. His investigations showed that this disease was very similar to Linford's pea streak and pineapple yellow spot virus (*5*, *6*).

Snyder and Thomas (*12*) showed that the spotted wilt virus was infectious to sweet peas and produced a streaking of the stems. Stubbs (*13*) produced a similar symptom on garden peas with the tobacco ring spot virus.

MATERIALS AND METHODS

VIRUSES

Pea streak virus 1—This virus was obtained from garden pea plants grown at Arlington, Va., in 1934. As mentioned previously, the disease appeared after pea aphids collected from alfalfa plants growing under field conditions were released in the greenhouse. This virus, when inoculated into pea and *Vicia faba*, produced a decided streaking of the stem, petioles, and leaf veins. Since the pea streak virus described by Linford does not appear to be a characteristic legume virus, the virus described in this paper is designated as pea streak virus 1.

Alfalfa mosaic virus 1—Viruses from three alfalfa mosaics were used in these studies; two were collected from mosaic-infected plants grown at Arlington, Va., and one from northeastern Colorado. One of the viruses secured in Virginia was apparently identical with the alfalfa virus described by Weimer (*16*), Pierce (*8*), and Zaumeyer and Wade (*20*). Pierce (*8*) was of the opinion that the alfalfa virus described by Weimer (*16*) and designated as alfalfa virus 1 was not identical with the virus described by him from the same host, which he listed as alfalfa virus 2. Subsequent studies by the writer suggest that these two viruses are identical. This virus will be discussed herein as alfalfa mosaic virus 1.

Alfalfa mosaic virus 1A.—The alfalfa virus collected from northeastern Colorado reacted similarly to alfalfa mosaic virus 1. Its specificity was established by the fact that it produced severer symptoms on peas and on *Vicia faba* than alfalfa mosaic virus 1, and by differences in host range and properties. The evidence presented in this paper indicates that this virus is a strain of alfalfa mosaic virus 1; it is designated here as alfalfa mosaic virus 1A.

Alfalfa mosaic virus 1B.—The third alfalfa mosaic virus was separated from material containing alfalfa mosaic virus 1. When a large number of pea plants of the Perfection variety were inoculated with alfalfa mosaic virus 1 all the plants except one manifested the typical mild mottling produced by alfalfa mosaic virus 1. This plant showed decidedly more extreme symptoms than the others, indicating a virus distinct from alfalfa mosaic virus 1. Symptomatology, host range, and properties in vitro showed the virus to be different from both alfalfa mosaic viruses 1 and 1A. This third virus is designated as alfalfa mosaic virus 1B.

METHODS

The experimental work was conducted in the greenhouse at approximately 14° to 21° C. when peas were inoculated and at 20° to 25° when beans were inoculated. The inoculum was secured from either

young infected peas or *Vicia faba* plants. Viruses from both hosts gave identical results. The virus extracts were prepared in the usual manner, by macerating diseased tissue in a sterile mortar and straining the juice. The solid residue was placed in cheesecloth and used as an inoculating pad. Leaflets of young plants were dusted with carborundum powder and rubbed with the pad saturated in the expressed mosaic-infected juice.

The methods used in the studies on thermal inactivation and on dilution were similar to those described by Johnson and Grant (*4*). The aging tests were made by storing the juice of infected plants in stoppered flasks in a darkened, constant-temperature chamber at 18° C. Inoculations were made at the desired intervals in the usual manner.

HOSTS

The principal hosts used in the differential studies of the viruses were garden peas, *Vicia faba*, and beans. Since certain pea varieties show more extreme symptoms than others when inoculated with the several viruses, a few were selected as test varieties. These were a variety known as Capucijner, which is an edible-pod pea grown widely in the Netherlands; Mammoth Melting Sugar, another edible-pod variety; and Dwarf Telephone. The bean varieties used were Stringless Green Refugee, Corbett Refugee, Robust, and Great Northern U. I. No. 1. Other leguminous hosts used are mentioned in a later section.

EXPERIMENTAL RESULTS

The four viruses discussed in this paper are differentiated by (1) the symptoms they produce on peas and other hosts, (2) varietal differences in susceptibility of peas and beans, (3) host range, and (4) certain properties of the viruses in vitro.

SYMPTOMS

Pea Streak Virus 1 on Pea

The first symptom produced on pea plants by pea streak virus 1 is a slight purpling and streaking of the stem and the lower portion of the stipule (fig. 1, *E*). Later the stipules recurve, the leaflets tend to curl downward and to become distorted and twisted, and the veins are decidedly pronounced (*B*, *F*, *H*). The tendrils become gnarled and twisted. Mottling does not occur on the young leaves, but frequently a clearing of the veins and a slight chlorosis is noticeable. The internodes in the apical portion of the plant are shortened and the leaves, which are smaller than usual, do not unfold normally but show a rosetted condition (*D*). The streaking of the stems becomes more intense and later takes on a brownish discoloration, which may extend from the top to the bottom of the plant. The phloem tissue becomes necrotic and discolored. This discoloration may also involve the petioles and main veins of the leaflets. The leaves finally become flaccid, the tip of the plant begins to wilt (*I*), and the plant ultimately dies. It is believed that death is due not to the virus alone but to soil fungi that attack the plant after it becomes weakened by the virus. In some cases only the tip dies, the rest of the plant remaining chlorotic (*I*).

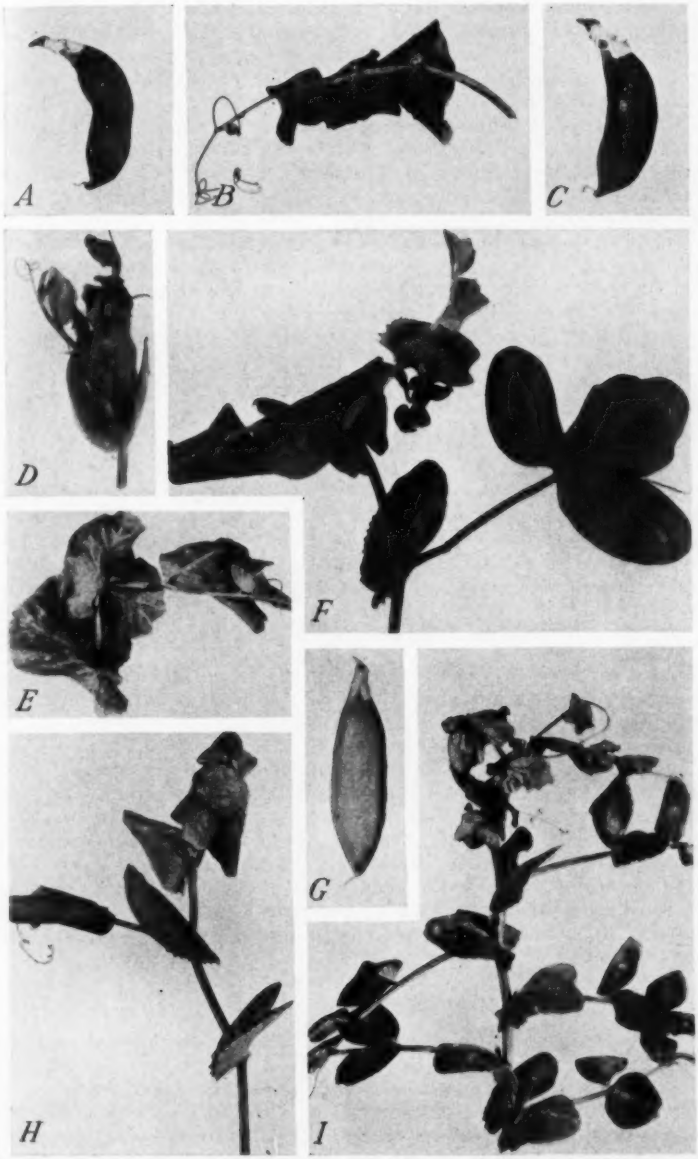

FIGURE 1.—Symptoms produced by pea streak virus 1 on several pea varieties: *A*, *C*, Pitting and spotting of World Record pea pods; *B*, *E*, downward curling of leaflets and streaking of petioles of Green Giant; *D*, terminal rosette and leaf malformation of Green Giant; *F*, infected Capucijner; *G*, healthy pod of World Record; *H*, stem streak and leaf curl of Capucijner; *I*, terminal killing of Admiral.

It frequently happens that a plant infected when young dies before attaining much growth. If it does not die, it is usually decidedly stunted, the leaves become curled and twisted and the veins very pronounced. Such plants are generally very brittle and when removed from the soil do not wilt as readily as do healthy plants.

Infected plants sometimes produce axillary buds, which usually die before much growth develops. When the virus is spread by aphids the symptoms first appear near the apical portion of the plant, but when the plants are artificially inoculated the symptoms are noted just above the point of inoculation.

The pods that are formed before the plant becomes seriously infected take on a dark purplish-gray or brown color over a considerable portion of their surface, but especially along the region of the dorsal suture. They may also be spotted, pitted, and decidedly malformed, and frequently do not reach maturity (fig. 1, *A* and *C*). Seeds from infected pods generally are small and shriveled.

Alfalfa Mosaic Viruses on Alfalfa

The symptoms of alfalfa mosaic viruses 1, 1A, and 1B on alfalfa are identical (fig. 2, *B*). The mosaic is first noted as small, light-greenish or light-yellow areas between or along the veins. Later these chlorotic regions enlarge and become increasingly more yellow in color. Distortion of infected leaves is not uncommon. At high temperatures the symptoms are commonly masked and diseased plants appear normal. The symptoms are most pronounced in the spring and early fall.

Alfalfa Mosaic Virus 1 on Pea

The symptoms produced on pea plants by alfalfa mosaic virus 1 appear in about 8 days after inoculation at 70° to 75° F. At lower temperatures that are more favorable for pea growth they do not develop so quickly and may require 10 to 15 days.

The first apparent symptom is a slight mottling that starts as small, chlorotic areas on the leaves above the point of inoculation. On some varieties these chlorotic areas may be very indistinct, while on others they may be more clearly defined. This mild chlorosis gradually becomes a mild mottling, light-green areas without pattern being found throughout the leaf. The leaves are not yellowed, the stems are not discolored as with pea streak virus 1, and the plants are not stunted. In general the symptoms produced by this virus are very mild on peas (fig. 2, *G* and *J*).

Alfalfa Mosaic Virus 1A on Pea

The symptoms of alfalfa mosaic virus 1A on peas appear in about the same length of time as those produced by alfalfa mosaic virus 1 but are much more pronounced than the latter. In addition to the mottling, which is quite pronounced (fig. 2, *I* and *L*), considerable leaf necrosis occurs. Infected leaves are slightly bronzed and frequently die. The stems appear purple but less strikingly so than in plants infected with pea streak virus 1. On the Dwarf Telephone variety, the symptoms of alfalfa mosaic virus 1A are very striking. The stunting of infected plants is possibly the most conspicuous symptom. The leaves are crinkled, the internodes are decidedly shortened, and

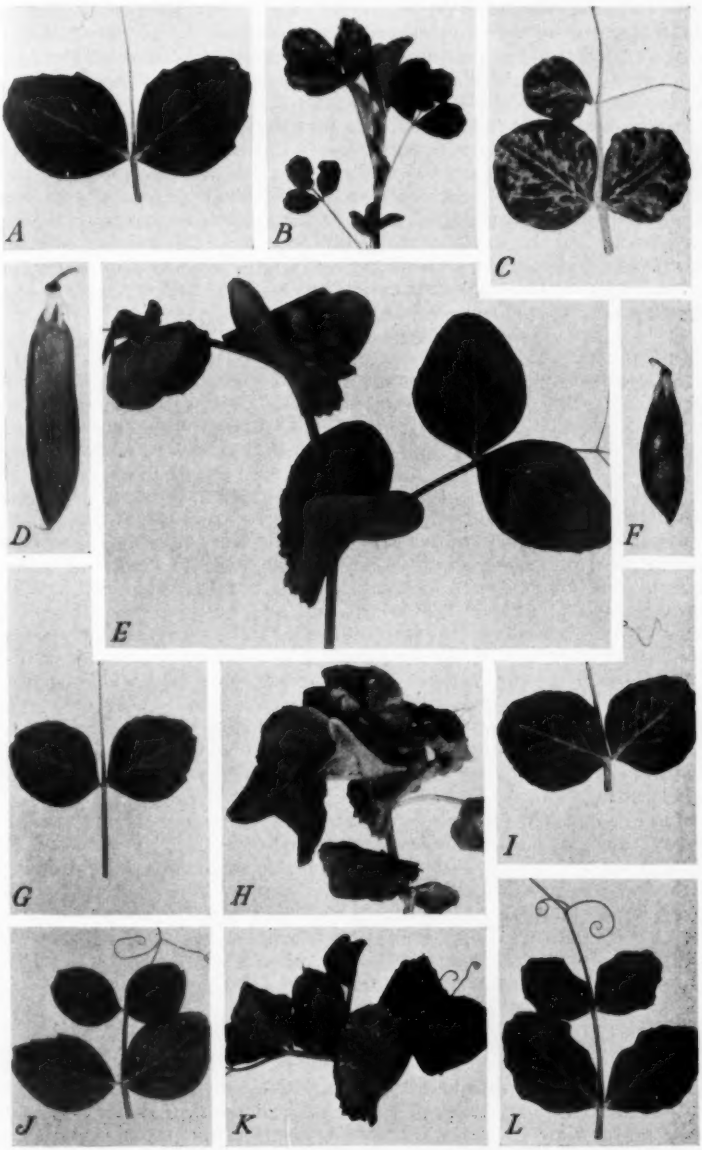

FIGURE 2.—Symptoms produced by the alfalfa mosaic viruses on alfalfa and pea: *A*, Healthy leaflets of Capucijner pea; *B*, mosaic-infected alfalfa; *C*, *E*, *K*, symptom variations produced by alfalfa mosaic virus 1B on Capucijner pea; *D*, healthy pod of World Record pea; *F*, pod of World Record pea infected with alfalfa mosaic virus 1A; *G*, *J*, leaflets of Capucijner and Green Giant pea, respectively, infected with alfalfa mosaic virus 1; *H*, Dwarf Telephone pea infected with alfalfa mosaic virus 1B; *I*, *L*, Capucijner and Green Giant pea, respectively, infected with alfalfa mosaic virus 1A.

the stem is discolored. On the under side of the leaves the veins and veinlets are brownish and appear water-soaked. The brownish color is also noticeable on the upper side of the leaflets, more or less along the veins and veinlets. A purplish discoloration occurs at the base of the leaflets and stipules.

A plant infected when young becomes very bunchy and never grows to more than one-fourth normal size. The uppermost leaves curl or roll inward, and are wavy along the edges, crinkled, and slightly chlorotic. In some cases, the midvein of older leaves is depressed, with an arching of the lamina. The vascular system of infected plants is necrotic.

Infected pods in some cases show a slight to severe dark necrotic discoloration. They are frequently spotted, pitted, and malformed (fig. 2, *F*).

Alfalfa Mosaic Virus 1B on Pea

The symptoms of alfalfa mosaic virus 1B on peas appear in about 8 days, the same length of time after inoculation as those produced by alfalfa mosaic viruses 1 and 1A. The inoculated leaves of susceptible varieties frequently die. Spotting of the remaining leaves follows, the spots usually appearing at the second node above the point of inoculation. Small brown spots appear first on the under side of the stipules and leaflets (fig. 2, *K*), but later are quite pronounced on the entire upper side of the leaflets. Later these spots become necrotic, and an infected stipule or leaflet may be killed. As in plants infected with pea streak virus 1, the stipules recurve and the leaflets tend to curl downward and become distorted (*E*). The stems become streaked (*E*), but the streaks are short, neither so continuous nor so intense in color as those produced by pea streak virus 1. When the infection is serious, alfalfa mosaic virus 1B stunts the plant to about the same degree as does pea streak virus 1. The symptoms produced by alfalfa mosaic virus 1B differ from those by pea streak virus 1, in (1) a pronounced spotting of the leaves and petioles, (2) less streaking of the stem and petioles, and (3) less downward curling and malformation of the leaflets.

In addition to the foregoing symptoms, the leaves of certain varieties are mottled quite intensely with large light-green areas between the veins (fig. 2, *C*). Such leaves are frequently crinkled and malformed. In general, the mottling is more intense on plants infected with alfalfa mosaic virus 1B than on those infected with alfalfa mosaic viruses 1 and 1A. On Dwarf Telephone peas, alfalfa mosaic virus 1B does not produce such pronounced symptoms and does not stunt the plants so much as does alfalfa mosaic virus 1A.

RESISTANCE AND SUSCEPTIBILITY OF HOSTS

Peas

A relatively small number of pea varieties were inoculated with the viruses herein reported except in the case of pea streak virus 1, with which more than 40 varieties were tested. This paper records the results from only those varieties that were tested with the four viruses, the object being to show differences in the reaction of the several viruses as a means of differentiating them.

Seventeen varieties of peas were inoculated with the four viruses under greenhouse conditions (table 1). The seeds were planted in

benches, and the plants were inoculated in the usual manner, carborundum powder being used on the surface of the leaves, which were then rubbed with a cheesecloth pad saturated with an undiluted extract from plants infected with the several viruses.

Table 1 shows that all varieties were susceptible to pea streak virus 1. Thus far no variety tested, including many not reported herein, has shown immunity to this virus. In most cases 100 percent of the plants were infected, although a number of varieties showed moderate symptoms. Alderman and Green Admiral alone manifested mild symptoms.

Alfalfa mosaic virus 1 caused mild symptoms on all varieties except Horal, which was immune. The symptoms on Little Marvel were slightly more pronounced than those on any of the other varieties. Although a high percentage of the plants became infected, the percentage was not quite so high as with pea streak virus 1.

Alfalfa mosaic virus 1A likewise infected all varieties except Horal. The infection in general was more severe with this virus than with alfalfa mosaic virus 1. Of the 16 susceptible varieties, 3 showed severe, 8 moderate, and 5 mild symptoms. Three varieties, Alderman, Green Admiral, and Surprise, in addition to manifesting mild symptoms, showed a lower percentage of infection than any of the others.

TABLE 1.—*Susceptibility and resistance of several pea varieties to pea streak virus 1 and alfalfa mosaic viruses 1, 1A, and 1B*

Variety	Results of inoculation with—											
	Pea streak virus 1			Alfalfa mosaic virus								
				1			1A			1B		
	Plants inoculated	Plants infected	Extent of infection [1]	Plants inoculated	Plants infected	Extent of infection [1]	Plants inoculated	Plants infected	Extent of infection [1]	Plants inoculated	Plants infected	Extent of infection [1]
	Number	*Number*		*Number*	*Number*		*Number*	*Number*		*Number*	*Number*	
Alaska	12	12	a	26	26	c	10	10	a	12	12	a
Alderman	16	11	c	12	10	c	13	5	c	14	14	b
Black Eye Marrow	9	9	a	10	9	c	9	9	b	12	12	a
Capucijner	20	20	a	13	13	c	9	7	c	10	10	a
Dwarf Telephone	12	12	a	47	41	c	36	36	a	10	10	b
Green Admiral	22	22	c	17	14	c	10	3	c	11	11	b
Green Giant	22	22	a	12	10	c	19	19	b	10	10	a
Harrison Glory	20	20	a	22	17	c	36	36	b	10	7	a
Horal	23	23	a	14	0	----	13	0	----	19	0	----
Laxton Progress	10	9	a	10	10	c	14	14	a	13	12	c
Little Marvel	10	10	a	10	9	b	20	18	c	26	26	b
Mammoth Melting Sugar	25	25	a	28	28	c	15	15	b	15	15	b
Perfection	31	31	a	28	28	c	12	12	b	19	19	a
Surprise	15	11	b	12	11	c	16	4	c	11	11	b
White Eye Marrow	21	19	b	19	12	c	10	10	b	10	10	a
Wisconsin Early Sweet	14	14	b	12	12	c	12	12	b	14	14	a
World Record	10	10	b	28	18	c	10	10	b	13	13	a

[1] a, serious infection; b, moderate infection; c, mild infection.

Horal was the only variety not susceptible to alfalfa mosaic virus 1B. In this respect alfalfa mosaic virus 1B reacts in the same way as alfalfa mosaic viruses 1 and 1A. The percentage of plants infected by alfalfa mosaic virus 1B was about equal to that infected by alfalfa

mosaic virus 1, but greater than that infected by alfalfa mosaic virus 1A. The symptoms produced on most varieties of peas by alfalfa mosaic virus 1B were more severe than those produced by the other two strains of alfalfa mosaic virus. Nine varieties showed severe symptoms, six moderate symptoms, and only one, Laxton Progress, mild symptoms.

Although in general the symptoms produced by alfalfa mosaic virus 1B were severer than those produced by alfalfa mosaic viruses 1 and 1A, there were a few exceptions. These seem to be significant in that they afford further aid in distinguishing the alfalfa mosaic viruses.

It was pointed out elsewhere that the Dwarf Telephone variety exhibited the severest symptoms when inoculated with alfalfa mosaic virus 1A; these are a decided stunting of the plant and an intense mottling followed by a crinkling of the leaves. Alfalfa mosaic virus 1 produces a very mild mottling and no stunting; in these respects alfalfa mosaic virus 1B is similar to alfalfa mosaic virus 1, but in addition the former causes a leaf spotting and a slight streaking of the stems.

On Laxton Progress, alfalfa mosaic virus 1A produced the severest leaf mottling, while alfalfa mosaic viruses 1 and 1B produced a mild mottling of about equal intensity.

On Little Marvel, alfalfa mosaic virus 1B produced the strongest leaf mottling of any of the viruses, followed next by alfalfa mosaic virus 1; alfalfa mosaic virus 1A produced the mildest mottling. The last mentioned virus, however, stunted the plants more severely than did the other two.

Beans

The bean varieties tested with the four viruses were Stringless Green Refugee, Corbett Refugee, Robust, and Great Northern U. I. No. 1 (table 2). All of these varieties, except Stringless Green Refugee, are resistant to the common bean mosaic virus. Twenty plants of each variety were inoculated with the pea streak virus and three lots, of 10 plants each, of each variety were inoculated with the three alfalfa mosaic viruses, respectively. The inoculations were made by lightly rubbing the leaves with an undiluted extract of the viruses. Carborundum powder was applied only with the pea streak virus. Since the alfalfa mosaic viruses produce local necrotic lesions on beans (fig. 3, *D* and *E*), the lesions on 20 inoculated leaves were counted to determine the degree of susceptibility. Where the lesions were very numerous, as in the case of Stringless Green Refugee, the number was estimated.

None of the four varieties was infected by pea streak virus 1. Alfalfa mosaic viruses 1, 1A, and 1B were infectious to all of the varieties (table 2). Stringless Green Refugee was the most susceptible to the three alfalfa mosaic viruses, as determined by the total number of local lesions produced; Great Northern U. I. No. 1 was next in susceptibility; Corbett Refugee and Robust showed about the same reaction. Alfalfa mosaic virus 1B produced fewer lesions on Stringless Green Refugee but a greater number of lesions on the other three varieties than did alfalfa mosaic virus 1A. Alfalfa mosaic virus 1 produced the smallest number of lesions on all varieties tested.

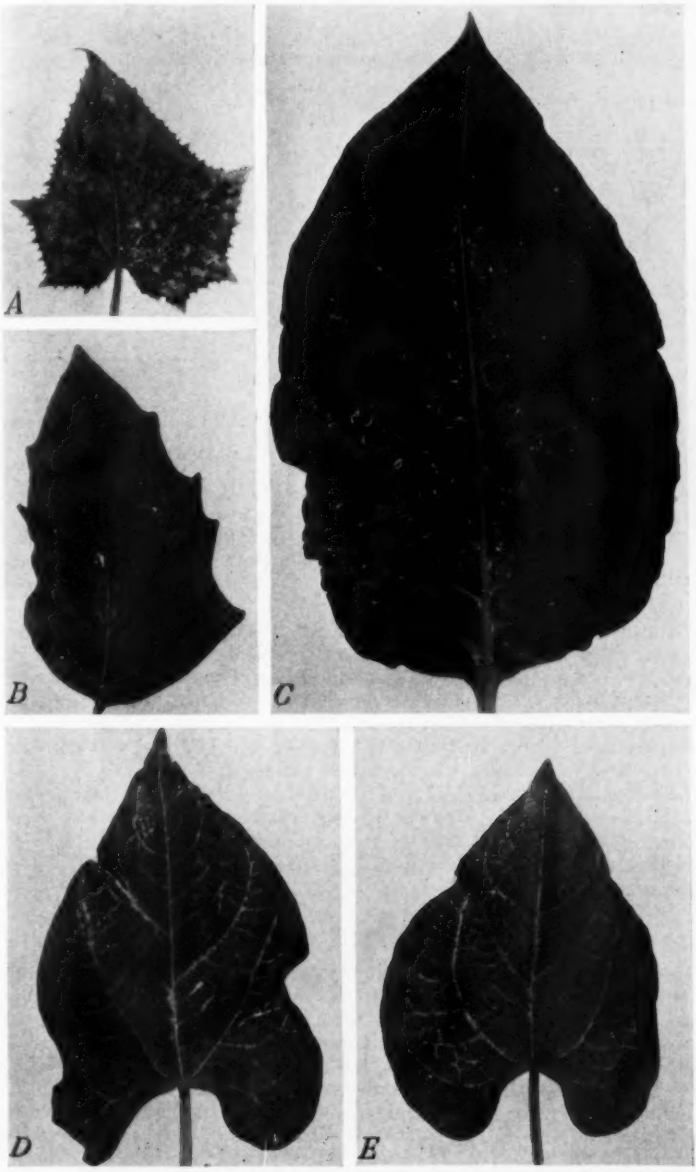

FIGURE 3.—Symptoms produced by alfalfa mosaic viruses on several hosts: *A*, Leaf mottling on cucumber produced by alfalfa mosaic virus 1A; *B*, mottling on *Datura stramonium* infected with alfalfa mosaic virus 1B; *C*, leaf pattern produced by alfalfa mosaic virus 1B on Turkish tobacco; *D*, *E*, local lesions produced by alfalfa mosaic viruses 1 and 1A, respectively, on Stringless Green Refugee bean; note higher percentage of light-tan centers of lesions in *E* than *D*.

TABLE 2.—*Susceptibility and resistance of four bean varieties to pea streak virus 1 and alfalfa mosaic viruses 1, 1A, and 1B*

Variety	Reaction[1] to—							
	Pea streak virus 1		Alfalfa mosaic virus					
			1		1A		1B	
	Plants inoculated	Plants infected	Plants inoculated	Total lesions[1]	Plants inoculated	Total lesions[1]	Plants inoculated	Total lesions[1]
	Number	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
Stringless Green Refugee	20	0	10	1,540	10	8,500	10	3,700
Corbett Refugee	20	0	10	26	10	82	10	235
Great Northern U. I. No. 1	20	0	10	35	10	237	10	506
Robust	20	0	10	29	10	71	10	258

[1] Total number of lesions produced on 20 inoculated primary leaves.

The size of the lesion varies, depending on the virus and the variety inoculated. On Stringless Green Refugee alfalfa mosaic virus 1 produced lesions from 1μ to 1½μ in diameter. The lesions produced by alfalfa mosaic viruses 1A and 1B on this variety averaged about 2μ in diameter. On Corbett Refugee the lesions were slightly smaller than on Stringless Green Refugee. On Robust and Great Northern U. I. No. 1, the lesions produced by alfalfa mosaic virus 1 were from 2μ to 2½μ in diameter, while those produced by alfalfa mosaic viruses A1 and 1B averaged approximately 2½μ to 3μ in diameter.

In addition to the production of local necrotic lesions, the alfalfa mosaic viruses frequently followed the veins and veinlets, causing them to become necrotic. This infection did not extend beyond the inoculated leaves. Alfalfa mosaic virus 1 produced only a slight vein necrosis on the inoculated leaves of Stringless Green Refugee, Corbett Refugee, and Great Northern U. I. No. 1. On Robust more vein necrosis was noted than on the other varieties.

Alfalfa mosaic viruses 1A and 1B produced more vein necrosis than alfalfa mosaic virus 1. On the Robust variety the former two viruses produced this type of infection more severely than on the other varieties. The necrosis frequently extended for a distance of 8μ to 10μ along veins and veinlets.

OTHER HOSTS

In order to determine the host range of the four viruses, a number of species in the genus *Phaseolus*, as well as species in other genera, were inoculated with the pea streak virus and with alfalfa mosaic viruses 1, 1A, and 1B, with results as shown in table 3.

It is evident from table 3 that the host range of pea streak virus 1 is more limited than that of the three strains of alfalfa mosaic virus. The following hosts were susceptible to pea streak virus 1: *Cicer arietinum*, *Lens esculenta*, *Medicago sativa*, *Melilotus alba*, *Soja max*, *Trifolium incarnatum*, *T. pratense*, *T. repens*, *Vicia faba*, *V. faba minor*, and *V. sativa*. In addition, alfalfa mosaic virus 1 was infectious to *Lupinus albus*, *L. luteus*, *Phaseolus angularis*, *P. aureus*, *P. lunatus*, *P. mungo*, *Vigna sesquipedalis*, *V. villosa*, *V. sinensis*, *Nicotiana tabacum*, *Petunia hybrida*, and *Datura stramonium*. This host range is more ex-

tended than that reported earlier for the same virus by Zaumeyer and Wade (*20*). It corresponds in general with that of Pierce (*8*), who tested a number of plant species with an alfalfa mosaic virus.

TABLE 3.—*Susceptibility and resistance of various legumes and other plants to pea streak virus 1 and alfalfa mosaic viruses 1, 1A, and 1B*

Plant	Reaction [1] to—							
	Pea streak virus 1		Alfalfa mosaic virus					
			1		1A		1B	
	Plants inoculated	Plants infected	Plants inoculated	Plants infected	Plants inoculated	Plants infected	Plants inoculated	Plants infected
	Number	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
Cajanus indicus Spreng. (pigeonpea)	7	0	8	0	5	0	10	0
Cicer arietinum L. (chickpea)	5	5	10	9D	10	8D	10	10D
Lathyrus odoratus L. (sweet pea, Pink Cockade variety)	10	0	15	0	20	8	15	0
Lens esculenta Moench (lentil)	16	10	20	18D	20	20D	20	20D
Lespedeza striata (Thunb.) Hook. and Arn. (lespedeza)	5	0	5	0	5	1	5	2
Lupinus albus L. (white lupine)	6	0	15	15L	18	18L	10	10L
L. luteus L. (lupine)	10	0	10	10	5	5	10	9
Medicago sativa L. (alfalfa)	5	2	5	1	5	3	5	2
Melilotus alba Desr. (white sweetclover)	5	4D	5	1D	5	1D	5	4D
Phaseolus acutifolius latifolius Freeman (tepary bean)	9	0	15	0	15	0	15	0
P. angularis (Willd.) W. F. Wight (adzuki bean)	11	0	10	8	10	10	10	10
P. aureus Roxb. (mung bean)	12	0	10	10L	15	15L	12	12L
P. calcaratus Roxb. (rice bean)	6	0	15	0	17	0	12	0
P. lunatus macrocarpus Benth. (lima bean)	5	0	5	0	5	0	10	0
P. lunatus L. (sieva bean, Henderson Bush variety)	5	0	10	9	12	12	10	10
P. mungo L. (urd bean)	20	0	9	2L	21	17	12	8L
Soja max (L.) Piper (soybean)	10	10	10	10	15	14	10	10
Stizolobium deeringianum Bort. (velvetbean)	5	0	10	0	10	0	9	0
Trifolium incarnatum L. (crimson clover)	5	4	5	5	5	3	5	5
T. pratense L. (red clover)	5	2	5	1	5	4	5	4
T. repens L. (white clover)	5	3	5	1	5	1		
Vicia faba L. (broadbean)	10	10 L	10	10 L	10	10 L	10	10 L
V. faba minor (small-seeded broadbean)	10	10 L	10	10 L	9	9 L	12	12 L
V. sativa L. (spring vetch)	16	11 L	10	8 L	10	8 L	12	10 L
V. villosa L. (vetch)	20	0	20	16 L	20	18 L	18	18 L
Vigna sesquipedalis (L.) Fruwirth (asparagus-bean)	12	0	10	10 L	10	10 L	10	10 L
V. sinensis (L.) Endl. (cowpea)	7	0	10	10 L	10	10 L	10	10 L
Nicotiana tabacum L. (Turkish tobacco)	5	0	5	5 L	5	5 L	5	5 L
Petunia hybrida Vilm. (petunia)	5	0	5	5	5	5	5	5
Datura stramonium L. (jimsonweed)	5	0	5	5	5	5	5	5
Lycopersicon esculentum Mill. (tomato)	5	0	5	0	5	0	5	0
Solanum tuberosum L. (potato)	5	0						
S. melongela L. (eggplant)	5	0	5	0	5	0	5	0
Capsicum annuum L. (pepper)	5	0						
Zinnia elegans Jacq. (zinnia)	5	0	10	0	13	1	10	4
Cucumis sativus L. (cucumber)	5	0	10	0	10	8	10	8

[1] D represents death of plants; L, local lesions.

Alfalfa mosaic virus 1A was infectious to the hosts just mentioned and in addition to *Cucumis sativus*, *Lathyrus odoratus*, *Lespedeza striata* and *Zinnia elegans*. Alfalfa mosaic virus 1B infected all the hosts that were susceptible to alfalfa mosaic virus 1A except *Lathyrus odoratus*.

SYMPTOMS OF THE VIRUSES ON DIFFERENTIAL HOSTS

It is not intended in this paper to describe in detail the symptoms produced by the several viruses on all the hosts that were inoculated with the four viruses. Certain distinct differences were noted on a number of hosts, both as to type of infection and severity of symptoms produced. It is believed that these differences are helpful in the differentiation and identification of the viruses.

On *Vicia faba* pea streak virus 1 produces very characteristic symptoms. The first symptom that appears is a local ring spot lesion, 3 to 5 mm in diameter, on the inoculated leaves (fig. 4, *C* and E), followed by a slight red to brown streaking of the stems (*A*). The stem streak progresses and may extend from the ground line to the uppermost tip of the plant, covering in some cases almost the entire stem (*F*). The petioles may also be streaked (*D*), as well as the veinlets on the under side of the leaflets.

On certain of the lower leaves of *Vicia faba* plants infected with pea streak virus, the circular ring spot lesions may cover a part or the whole of a leaflet (fig. 4, *C* and *E*). In other cases circular zonate spots appear which may coalesce with others, producing large dark-gray to black spots resembling the lesions produced by *Alternaria* sp. These areas are surrounded by a yellowish border and may appear in the center of the leaflet, but most frequently they are found along the margins of the leaf. If the lesions are large, the infected leaflet may wither and die (*F*).

The tips of *Vicia faba* plants infected with pea streak virus 1 are often rosetted. The leaves are smaller than normal, do not unfold properly, and are spotted and streaked (fig. 4, *B*). The plants may gradually die, beginning at the growing point, and in such cases the stem may show only a small amount of streaking (*B*). In other cases the entire stem may be reddened, normal-appearing leaflets being found below the dead tissue (*F*).

Alfalfa mosaic virus 1 also produces local, necrotic, reddish to brownish lesions on *Vicia faba*. The inoculated leaves later die. The uppermost leaves curl inward and show a stippled bronzing that later becomes a more distinct, reddish spotting. The spots are usually more numerous at the base of the leaflet (fig. 5, *E*). These leaves frequently die while some of the lower leaves still appear normal. The stem may be shrunken and decidedly streaked, the streaks being blackish brown. Seriously infected plants usually die.

The symptoms produced by alfalfa mosaic viruses 1A and 1B on *Vicia faba* are essentially the same as those produced by alfalfa mosaic virus 1, except that they are more severe. Alfalfa virus 1B produces the most striking symptoms. The local necrotic lesions produced by this virus on the inoculated leaves are larger and more numerous than those produced by either of the other alfalfa mosaic viruses (fig. 5, *B*). These lesions may cover an entire leaflet, causing it to die 5 days after the appearance of symptoms. The tip of the plant (*C*) frequently shows the effect of infection shortly after the local lesions appear on the inoculated leaves (*B*), and often it is killed 10 to 12 days after inoculation. The stem then begins to shrink, takes on a black discoloration (*C*), and becomes internally necrotic.

As already mentioned, the pea streak virus is not infectious to bean, whereas the three alfalfa mosaic viruses produce local necrotic lesions on the inoculated leaves (fig. 3, *D* and *E*). The only differ-

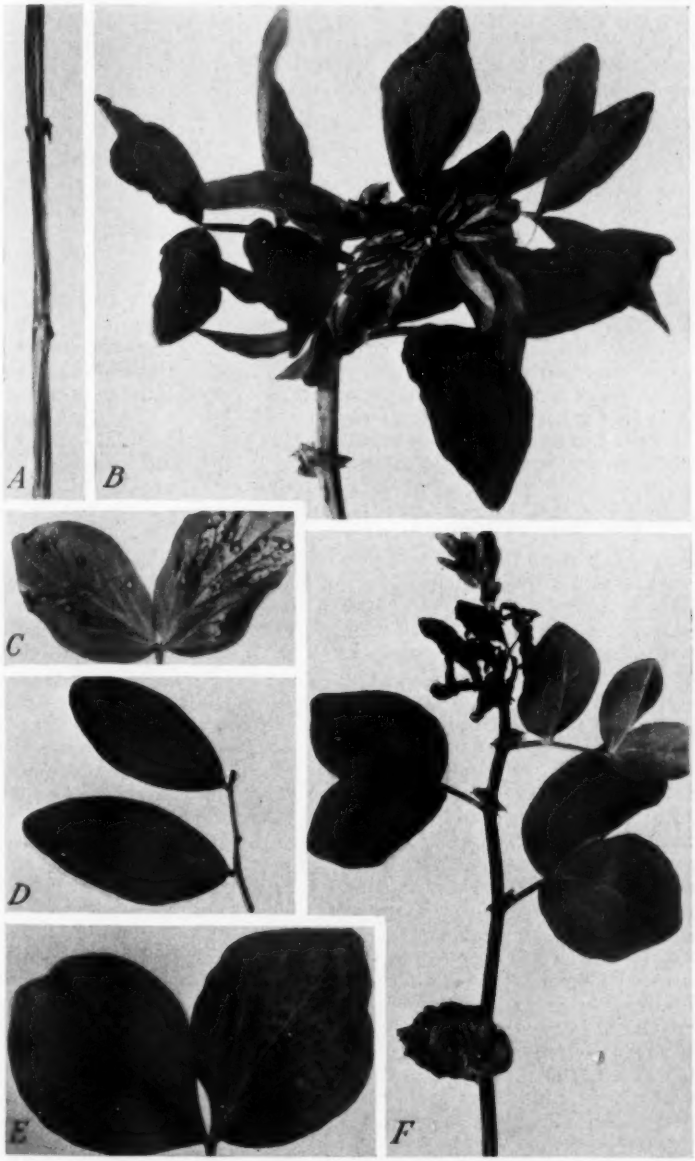

FIGURE 4.—Symptoms produced by pea streak virus 1 on Windsor broadbean: *A*, streaking of stem; *B*, leaf spot and rosette; *C*, *D*, *E*, ring-spot-like symptoms on leaflets; *F*, stem streaking and killing of inoculated and terminal leaflets; center leaflets appear normal.

ences between the symptoms produced by the latter viruses on bean were in the size of the lesions produced and in the formation of light-tan centers. The local lesions produced by alfalfa mosaic virus 1 never exceeded 1 to 2½ mm in diameter and were brownish red, with only an occasional light-tan center (*D*). Alfalfa mosaic viruses 1A (*E*) and 1B produced lesions 2 to 3 mm in diameter with a high percentage of light-tan centers.

On white sweetclover, pea streak virus 1 and alfalfa mosaic viruses 1 and 1A produced a mild mottling. The infected plants became generally chlorotic and died. Alfalfa mosaic virus 1B produced local lesions on the inoculated leaves. The infected plants were decidedly stunted, became chlorotic, and died.

On crimson clover, pea streak virus 1 produced a marked mottling of the leaves (fig. 5, *O*), while alfalfa mosaic virus 1 produced a very mild mottling which frequently was difficult to diagnose. Alfalfa mosaic virus 1A produced an extreme mottling (*P*), the leaves being smaller than normal (*K*) and the plant stunted. Alfalfa mosaic virus 1B produced severe mottling, spotting, crinkling, and malformation of the leaves and a stunting of the plant (*M*).

On red clover, pea streak virus 1 produced a fairly distinct mottling. Alfalfa mosaic virus 1 manifested itself as a very mild mottling, while alfalfa mosaic virus 1A produced a mottling equal in intensity to that produced by pea streak virus 1. Alfalfa mosaic virus 1B likewise produced a distinct mottling and in addition a leaf spotting (fig. 5, *G*) similar to that on crimson clover. In this respect alfalfa mosaic virus 1B is distinctly different from any of the other viruses.

White lupine was resistant to pea streak virus 1, which can thus be distinguished from the other viruses. On white lupine the alfalfa mosaic viruses produced local lesions (fig. 5, *J* and *L*) that differed in size and number. Alfalfa mosaic virus 1 produced the smallest lesions and the fewest per unit area of leaf surface; alfalfa mosaic virus 1A produced the largest lesions and the greatest number per unit area. The inoculated leaves were killed most readily when inoculated with alfalfa mosaic virus 1A. The systemic symptoms produced by alfalfa mosaic virus 1 were a mild leaf mottling and a slight chlorosis. Alfalfa mosaic virus 1A produced a distinct mottling and considerable chlorosis. The uppermost leaves were small, puckered, distorted, and curled upward. Infected plants were decidedly stunted, and the growing tip was frequently killed. Alfalfa mosaic virus 1B produced symptoms slightly more pronounced than those produced by alfalfa mosaic virus 1.

Soybean was resistant to pea streak virus 1. Alfalfa mosaic virus 1 produced a stunting of the plant and a decided mottling, puckering, crinkling, arching, and downward curling of the leaflets; alfalfa mosaic virus 1A produced similar but slightly more intense symptoms (fig. 5, *D*). The youngest trifoliate leaves showed necrosis and frequently were killed; the plants, however, did not die. Alfalfa mosaic virus 1B produced symptoms more severe than those produced by alfalfa mosaic virus 1 but not so intense as those produced by alfalfa mosaic virus 1A.

The only virus that infected sweet pea was alfalfa mosaic virus 1A. The only symptom was a leaf mottling.

Alfalfa mosaic viruses 1A and 1B infected zinnia, producing a definite mottling of the leaves.

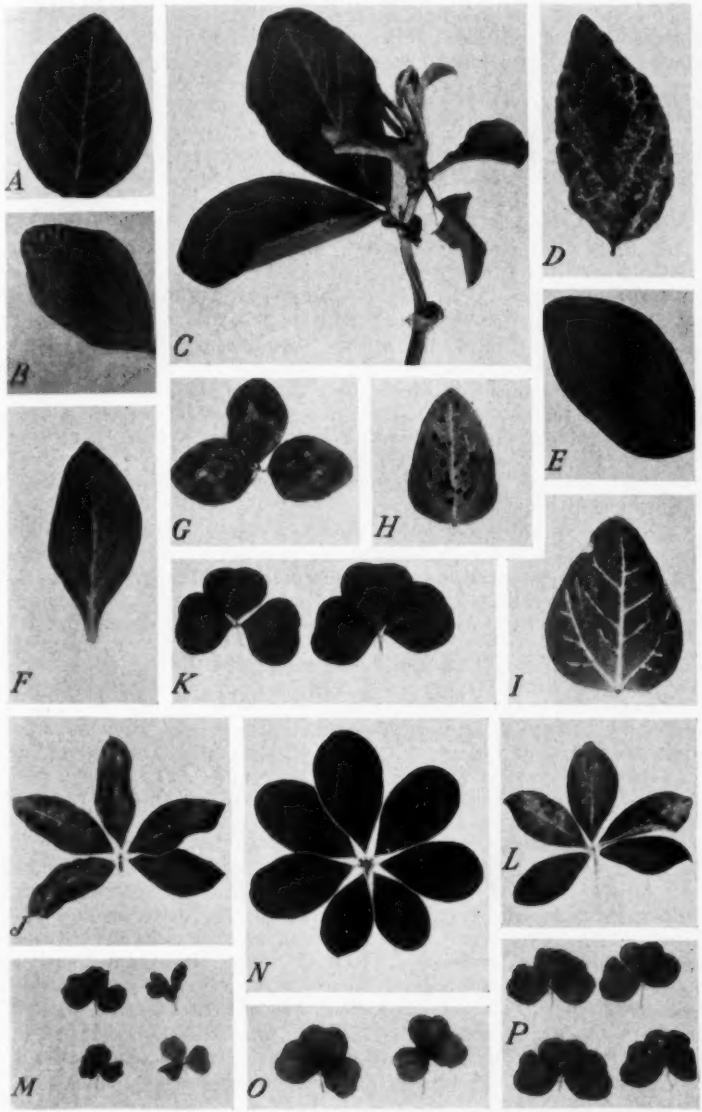

FIGURE 5.—Symptoms produced by pea streak virus 1 and alfalfa mosaic viruses on different hosts: *A*, Healthy soybean leaflet; *B*, *C*, variations in symptoms produced by alfalfa mosaic virus 1B on Windsor broadbean; *D*, mottling on soybean infected with alfalfa mosaic virus 1A; *E*, leaf spot on Windsor broadbean infected with alfalfa mosaic virus 1; *F*, mottling on petunia leaf caused by alfalfa mosaic virus 1A; *G*, red clover leaves infected with alfalfa mosaic virus 1B; *H*, *I*, local lesions produced by alfalfa mosaic viruses 1A and 1B, respectively, on Black Eye cowpea; *J*, *L*, white lupine infected with alfalfa mosaic viruses 1A and 1B, respectively; *K*, healthy crimson clover; *M*, *O*, *P*, crimson clover infected with alfalfa mosaic virus 1B, pea streak virus 1, and alfalfa mosaic virus 1A, respectively; *N*, healthy white lupine.

Tobacco was not infected by pea streak virus 1; the three alfalfa mosaic viruses produced similar symptoms, namely, white necrotic flecks and small rings and arcs on the inoculated leaves. A mottling later developed and was followed by necrotic areas similar to the oak-leaf pattern (fig. 3, *C*) of the tobacco ring spot virus described by Fromme et al. (*1*). The only symptomatological difference between the three viruses was in the intensity of the mottling. Alfalfa mosaic virus 1 produced the mildest mottling, and alfalfa mosaic virus 1A the most pronounced.

Jimsonweed was resistant to the pea streak virus but susceptible to the three alfalfa mosaic viruses. Alfalfa mosaic virus 1 produced a mild mottling, alfalfa mosaic virus 1A an intense mottling, and alfalfa mosaic virus 1B a still more intense mottling (fig. 3, *B*). The last-named virus produced also brown necrotic spots, which first appeared at the tip and later spread throughout the entire leaflet.

Petunia was not infected by the pea streak virus, but was susceptible to the three strains of alfalfa mosaic, each producing a decided mottling of the leaves. Alfalfa mosaic virus 1 caused the least intense mottling, while alfalfa mosaic viruses 1A and 1B produced severe mottling of about equal intensity (fig. 5, *F*). The leaves of the plants infected with alfalfa mosaic virus 1B were small, somewhat distorted, and necrotic.

Cucumber was infected only by alfalfa mosaic viruses 1A and 1B. The symptoms appeared on the young leaves as small chlorotic spots that gradually enlarged, causing a mild leaf mottling. On the later formed leaves, yellowish-green spots appeared throughout the leaf (fig. 3, *A*). Such leaves frequently showed extreme distortion.

PROPERTIES OF THE VIRUSES

Although the properties of alfalfa mosaic virus 1 had been previously studied by Pierce (*8*) and Zaumeyer and Wade (*20*), they were again determined in order to get a direct comparison of the properties of this virus with those of the pea streak virus and alfalfa mosaic viruses 1A and 1B. The thermal inactivation points, resistance to aging in vitro, and tolerance to dilution of the four viruses were studied for the purpose of determining differences as a means of separating and identifying them. In the case of the pea streak virus, the studies were made with peas as the test host. The determinations with alfalfa mosaic viruses 1 and 1A were made with beans because of the ability of the viruses to produce local necrotic lesions on them. In the trials with alfalfa mosaic virus 1B, both beans and peas were used. The routine methods described by Johnson and Grant (*4*) were employed; the only variation was in the aging tests. The viruses were stored in stoppered flasks and placed in a darkened constant-temperature chamber maintained at 20° C., whereas Johnson and Grant stored their viruses at temperatures ranging from 80° to 90° F.

Thermal Inactivation Point

The thermal inactivation point of pea streak virus 1 was found to be between 62° and 65° C. when heated for 10 minutes (table 4). Alfalfa mosaic virus 1 was inactivated between 65° and 70°. This is slightly higher than the inactivation point reported for the same virus by Pierce (*8*) and Zaumeyer and Wade (*20*), who found it to be

between 62° and 65°. Alfalfa mosaic virus 1A lost its infectivity at the same points as alfalfa virus 1. Alfalfa virus 1B was inactivated at 70° to 75°.

TABLE 4.—*Comparison of the thermal inactivation points of pea streak virus 1 alfalfa mosaic virus 1, alfalfa mosaic virus 1A, and alfalfa mosaic virus 1B*

Temperature (° C.)	Pea streak virus 1 on pea, systemic infection		Alfalfa mosaic virus				
			1 on bean, total lesions [1] produced by local infection	1A on bean, total lesions [1] produced by local infection	1B on—		
					Bean, total lesions [1] produced by local infection	Pea, systemic infection	
	Plants inoculated	Plants infected				Plants inoculated	Plants infected
	Number	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
Not heated	20	20	5,860	5,880	4,560	12	12
58	25	7					
60	27	7	5,560	4,980		12	12
62	21	2	4,030	4,620	4,220	12	12
65	24	0	80	620	98	12	10
70	25	0	0	0	9	12	2
75						10	0

[1] Total number of lesions produced on 20 inoculated primary leaves of Stringless Green Refugee bean variety.

Resistance to Aging in Vitro

Pea streak virus 1 was noninfectious when aged 2 days at 20° C. (table 5); alfalfa mosaic virus 1 was inactivated after aging 4 to 5 days. This is not in agreement with Pierce (*8*), who reported the virus to be infectious after 8 to 9 days' aging at laboratory temperatures. Zaumeyer and Wade (*20*) previously reported the virus as living 3 to 4 days in vitro. Alfalfa mosaic viruses 1A and 1B were noninfectious after 4 to 5 days' aging.

Tolerance to Dilution

Table 6 shows that pea streak virus 1 was infectious at a dilution of 1 to 5,000. Alfalfa mosaic virus 1, however, lost its activity at a dilution greater than 1 to 2,000, which agrees with the results of both Pierce (*8*) and Zaumeyer and Wade (*20*). Alfalfa mosaic viruses 1A and 1B were infectious at a dilution of 1 to 3,000 but not at 1 to 5,000.

The differences in the properties of the several viruses seem to be sufficient to differentiate pea streak virus 1 from the alfalfa mosaic viruses. The thermal inactivation point for the pea streak virus was lower than that of the three strains of the alfalfa mosaic virus. Regarding aging in vitro, pea streak virus 1 lost its infectivity more rapidly, but tolerated a higher dilution than did the alfalfa mosaic viruses.

Alfalfa mosaic viruses 1, 1A, and 1B showed variations in their physical properties; these variations, however, were too slight to be of significance in differentiating the viruses. The only variation worth noting was that alfalfa mosaic virus 1B was inactivated at a slightly higher temperature than alfalfa mosaic viruses 1 and 1A.

TABLE 5.—*Comparison of resistance to aging in vitro of pea streak virus 1, alfalfa mosaic virus 1, alfalfa mosaic virus 1A, and alfalfa mosaic virus 1B*

Time aged at 20° C.	Pea streak virus 1 on pea, systemic infection		Alfalfa mosaic virus				
					1B on—		
	Plants inoculated	Plants infected	1 on bean, total lesions [1] produced by local infection	1A on bean, total lesions [1] produced by local infection	Bean, total lesions [1] produced by local infection	Pea, systemic infection	
						Plants inoculated	Plants infected
	Number	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
None	12	12	9,260	4,025	3,654	12	12
6 hours	13	12					
8 hours	13	11					
10 hours	14	10					
12 hours	15	8					
24 hours	11	1	30	140		12	12
2 days	11	0	3	4	4	10	1
3 days			5	4	2	12	0
4 days			3	3	2	12	2
5 days			0	0	0	10	0
7 days							

[1] Total number of lesions produced on 20 inoculated primary leaves of Refugee Green bean variety.

TABLE 6.—*Comparison of tolerance to dilution of pea streak virus 1, alfalfa mosaic virus 1, alfalfa mosaic virus 1A, and alfalfa mosaic virus 1B*

Dilution	Pea streak virus 1 on pea, systemic infection		Alfalfa virus 1 on bean, total lesions [1] produced by local infection	Alfalfa virus 1A on bean, total lesions [1] produced by local infection	Alfalfa virus 1B on—		
					Bean, total lesions [1] produced by local infection	Pea, systemic infection	
	Plants inoculated	Plants infected				Plants inoculated	Plants infected
	Number	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
None	20	20	9,860	4,730	14,100	10	10
1:500	23	18	30	29	96	10	10
1:1,000	21	14	6	32	11	10	8
1:2,000	22	11	3	7	2	13	9
1:3,000	28	12	0	4	2	13	2
1:5,000	17	6		0	0	14	0

[1] Total number of lesions produced on 20 inoculated primary leaves of Refugee Green bean variety.

SEPARATION OF THE VIRUSES

The separation of the several viruses may be accomplished by means of physical-property studies as well as by differences in host range.

Pea streak virus 1 can be separated from a mixture with the alfalfa mosaic viruses by inoculation to the Horal variety of peas, which is susceptible to the pea streak virus but immune to the three strains of alfalfa mosaic virus. On the other hand, it is possible to isolate the alfalfa mosaic viruses from a mixture with pea streak virus 1 by inoculating garden bean, soybean, cowpea, white lupine, tobacco, petunia, and jimsonweed, which are all susceptible to the three strains of alfalfa mosaic virus, but resistant to pea streak virus 1.

Aging the viruses in vitro over 25 hours at 18° C. will separate pea streak virus 1 from the alfalfa mosaic viruses, since the latter are active for about 3 days under such conditions, while pea streak virus 1 is inactivated when aged for more than 25 hours at 18°.

Although the three alfalfa mosaic viruses are distinguishable from one another on many hosts, it is difficult to separate them in a mixture.

Thus far no method has been found of recovering alfalfa mosaic virus 1 from a mixture with alfalfa mosaic viruses 1A and 1B. Alfalfa mosaic viruses 1A and 1B can be obtained from a mixture with alfalfa mosaic virus 1 by inoculating zinnia or cucumber, which are susceptible to alfalfa mosaic viruses 1A and 1B but resistant to alfalfa mosaic virus 1, or by diluting a virus mixture 1 to 3,000, a dilution at which alfalfa mosaic virus 1 is inactivated while the other two viruses are not.

Alfalfa mosaic virus 1A can be separated from alfalfa mosaic virus 1 and 1B by inoculating sweet pea, Pink Cockade variety, which is susceptible to alfalfa mosaic virus 1A but resistant to the other two viruses.

Alfalfa mosaic virus 1B produces a necrotic spotting of the leaves on many pea varieties. It can be separated from a mixture of the alfalfa mosaic viruses by diluting an extract 1 to 1,000 and inoculating the Capucijner pea variety, on which it produces a necrotic spotting of the leaves above the point of inoculation. By removing this necrotic tissue, reinoculating the same variety with the expressed juice of the necrotic tissue, and repeating this procedure, alfalfa mosaic virus 1B can be separated from alfalfa mosaic viruses 1 and 1 A.

DISCUSSION

Within the past few years a number of investigations (*7*, *8*, *13*, *17*, *20*, *21*, *22*) have shown that several distinct viruses are capable of infecting peas, beans, and other legumes. Certain of these viruses produce similar symptoms on various hosts and are therefore difficult to differentiate. Host range and property studies, together with symptomatological comparisons, have made it possible to name, describe, and classify certain of the viruses affecting legumes.

The evidence presented in this paper shows that, in addition to those viruses already described on legumes, still others are infectious to them. The data also show that the four viruses described can be differentiated, even though the symptoms they produce on certain hosts are in some cases and under certain conditions quite similar. In table 7 most of the outstanding differences in host reaction are noted.

TABLE 7.—*Summarized table for the differentiation and identification of pea streak virus 1 and alfalfa mosaic viruses 1, 1A, and 1B*

Virus	Type of infection	Reaction [1] of—															
		Phaseolus vulgaris (Stringless Green Refugee variety)	*Pisum sativum* (Perfection variety)	*Pisum sativum* (Horal variety)	*Vicia faba* (Windsor variety)	*Vigna sinensis* (Groit variety)	*Melilotus alba*	*Trifolium incarnatum*	*Trifolium pratense*	*Lupinus albus*	*Soja max*	*Lathyrus odoratus*	*Cucumis sativus*	*Datura stramonium*	*Nicotiana tabacum*	*Petunia hybrida*	*Zinnia elegans*
Pea streak virus 1	Local	—	—	—	b	—	c	a	b	—	—	—	—	—	—	—	—
	Systemic	a	a	b	a	—	—	—	—	c	—	—	—	—	—	—	—
Alfalfa mosaic virus 1.	Local	—	—	—	c	c	c	c	c	b	b	—	—	c	c	c	—
	Systemic	a	c	—	b	b	—	—	—	a	—	—	—	c	c	—	—
Alfalfa mosaic virus 1A.	Local	—	b	—	b	b	c	a	b	a	a	c	—	b	a	b	b
	Systemic	a	—	—	a	—	—	—	—	b	—	—	b	—	—	—	—
Alfalfa mosaic virus 1B.	Local	—	—	—	a	b	c	a	a	b	b	—	b	a	b	a	b
	Systemic	—	a	—	a	—	c	a	a	b	b	—	b	a	b	a	b

[1] Minus sign (—) represents no infection; a, severe infection; b, moderate infection; c, mild infection.

It is quite likely that some of the legume viruses thus far described, as well as others that may be described later, are not necessarily new viruses but are actually strains of some that have already been described, even though they may have been isolated from different hosts. For example, the three alfalfa mosaic viruses described here, though closely related, possess certain characteristics that distinguish them from one another. It is not unlikely that others will be found differing from those herein described.

Since 1928, a number of viruses causing pea streak have been reported. In comparing the symptoms produced by several of these, one might be led to believe that they are the same. Thus the symptoms of pea streak virus 1 described in this paper show marked similarity to those of the pea streak described by Linford [6] in the United States in 1928, and later from Hawaii. Linford (*5*) proved that the pea streak virus in Hawaii was identical with the yellow spot virus of pineapple and suggested that the pea streak in the United States may be caused by either this or a related virus. What appeared to be the same disease was observed by the writer in pea fields in Idaho, in 1932 and 1934. In 1934 it was also reported [7] from Montana, where a field of peas showed a considerable amount of infection, so much, in fact, that the yield was materially reduced. L. K. Jones, in a bulletin by Vincent (*14*), reported a pea streak virus in western Washington in 1935.

The present writer observed that infected pea plants were most commonly found in close proximity to alfalfa plants, either where volunteer alfalfa plants appeared in a pea field or where alfalfa was growing along the borders of a field. It was also reported [7] that the disease in Montana was found in a pea field planted to alfalfa in previous years and that a considerable number of volunteer alfalfa plants occurred there. No virus determination was possible at the time, so it is not known whether this disease was similar to the streak disease reported in this paper or to the disease which Linford (*5*) described on peas from Hawaii. Since alfalfa plants have been associated in most cases with the disease in the United States, it appears that these plants may have some logical connection with the disease. The alfalfa plants showed no signs of being infected with a virus, but the symptoms may have been masked, as is frequent under conditions of high temperature.

If the pea streak disease in the western part of the United States is the same as that reported by Linford (*5*, *6*) in Hawaii, it is distinctly different from pea streak virus 1 herein described. The pea streak virus from Hawaii is transmitted by *Thrips tabaci* and is not readily transmitted artificially. Pea streak virus 1 is transmitted by the pea aphid (*Illinoia pisi*) and in preliminary tests was not shown to be transmitted by *T. tabaci*. The virus is readily transmitted by artificial means.

The spotted wilt of garden pea reported by Whipple (*17*) appears to be the same disease as Linford's (*6*) pea streak and pineapple yellow spot. The symptoms of the spotted wilt virus on pea resemble those produced by pea streak virus 1, and the symptoms caused by the former virus on *Vicia faba*, as reported by Smith (*11*), resemble those of pea streak virus 1 on this host. However, differences in host range, properties, and transmission indicate that the viruses are not related.

[6] Linford, Maurice B. See footnote 3, p. 747.
[7] Correspondence in files of Division of Fruit and Vegetable Crops and Diseases.

Snyder's (*12*) spotted wilt of sweet pea is identical with Whipple's (*17*) virus of garden pea.

Pierce (*7*) isolated a virus from a red clover plant, which he named the broadbean local-lesion virus. When inoculated to broadbean, it produced local necrotic lesions but no systemic symptoms. He stated that the local-lesion virus, especially when in combination with other viruses, tends to produce streak symptoms on peas.

Although Pierce's (*7*) host-range studies with this virus were meager, there appear to be minor similarities between pea streak virus 1 and the broadbean local-lesion virus. Both viruses produce local necrotic lesions on *Vicia faba*, but pea streak virus 1 in addition becomes systemic. Both infected soybean but were not infectious to Stringless Green Refugee bean.

Regarding the properties of the viruses, the broadbean local-lesion virus is inactivated when heated for 10 minutes at 60° to 62° C., and on aging in vitro from 2 to 3 days. Pea streak virus 1 is inactivated on heating to 62° to 65° and on aging from 1 to 2 days.

It is probable that these viruses are similar and that the local-lesion virus of Pierce may be a less virulent strain of pea streak virus 1. A more comprehensive study of the host range and properties of the broadbean local-lesion virus is necessary before this can be definitely determined. The alfalfa mosaic viruses discussed in this paper differ distinctly from the broadbean local-lesion virus.

Alfalfa mosaic virus 1, reported in this paper, is identical with the alfalfa virus described by Weimer (*15*, *16*), as well as with the alfalfa virus reported by Zaumeyer and Wade (*20*). It is likewise the same virus as that described by Pierce (*8*) as alfalfa virus 2.

The viruses of white clover mosaic and sweetclover mosaic, producing streak symptoms on peas, reported by Zaumeyer and Wade (*19*, *22*) and Pierce (*7*), are dissimilar to the viruses described herein. Stubbs (*13*), who produced a streak symptom on peas with the tobacco ring spot virus, dealt with a virus unlike those described in this paper.

The alfalfa mosaic viruses discussed here are of peculiar interest because of their wide host range and because of the fact that the symptoms they produce on certain hosts are somewhat similar to those produced by other apparently unrelated viruses. As pointed out earlier, the alfalfa mosaic viruses infect certain hosts, outside of the family Leguminosae, which have not been shown to be infected by the previously described legume viruses.

The local lesions produced by the tobacco mosaic virus on beans, as shown by Price (*9*), are somewhat similar to though smaller than those produced by the alfalfa mosaic viruses. Similarly, the local necrotic lesions produced on cowpea by the various strains of cucumber mosaic, as pointed out by Price (*10*), are in general quite similar to the lesions of the alfalfa mosaic viruses on this host (fig. 5, *H* and *I*).

The alfalfa mosaic viruses produce on the inoculated leaves of Turkish tobacco small white rings and arcs, not unlike those produced by the course etch virus of Johnson (*3*) on burley tobacco. On the uppermost leaves they produce white concentric rings and patterns, resembling those produced by the ring spot virus from sweetclover described by Henderson (*2*).

On petunia the alfalfa mosaic viruses produce symptoms that resemble the early symptoms of the cucumber mosaic virus on this host.

They are, however, much less pronounced than the symptoms produced by the tobacco mosaic virus and the tobacco ring spot virus.

On *Datura stramonium* the symptoms of the alfalfa mosaic viruses slightly resemble those produced by the latent or X virus of potato.

The early mottling produced by the alfalfa mosaic viruses on cucumber is slightly similar to the mottling exhibited by cucumber mosaic. Later, however, the symptoms of the alfalfa mosaic viruses are more severe and are distinctly different from those produced by the cucumber virus. Infected plants are stunted and the leaves become dark green with small stipplelike chlorotic spots. Later formed leaves are decidedly puckered and savoyed and much smaller than normal. The yellow areas are not so well defined in leaves infected with cucumber mosaic virus as in those infected with the alfalfa mosaic viruses.

Insect transmission of the alfalfa mosaic viruses was not studied. It was shown that pea streak virus 1 was transmitted by the pea aphid, a feature which distinguished it from the spotted wilt virus. Weimer (*16*) showed that alfalfa virus 1 was transmitted from diseased to healthy alfalfa plants by the pea aphid. It is not unlikely that this aphid can transmit this virus, as well as alfalfa mosaic viruses 1A and 1B, to pea.

The economic importance of pea streak virus 1 is unknown. If the pea streak disease found by the writer and others in commercial fields is similar to pea streak virus 1 or to any of the alfalfa mosaic viruses, then it is of commercial importance.

Alfalfa mosaic is widespread and has been reported from many localities. The symptoms are quite noticeable in the spring and fall of the year throughout the eastern and midwestern United States where the disease has been found; but in summer, when the temperatures are high, it is difficult to diagnose. Infected plants appear normal under these conditions, but the virus is readily isolated from such plants. L. K. Jones (as reported by Vincent (*14*)) found alfalfa mosaic abundant in certain counties of Washington, and he believes that the disease causes a decline in vigor and possibly is a factor in winter injury of the plants.

The relationship of alfalfa mosaic to peas under field conditions is unknown. Because of the similarity of symptoms of the alfalfa mosaic viruses and certain of the other legume viruses on peas, it is not unlikely that the alfalfa mosaic may be responsible, in some localities, for at least part of the reported pea mosaic. Alfalfa mosaic has never been found to affect beans under field conditions and hence is no factor in crop production.

From the foregoing data, it is evident that the viruses herein described are different from those heretofore reported as infecting pea and that they can readily be distinguished from one another as well as from other viruses affecting pea.

SUMMARY

A new virus disease of pea, of the streak type, together with a comparison of three strains of alfalfa mosaic that are infectious to pea, bean, and other legumes, are described and identified.

The differentiation of the viruses was based on the expression of symptoms produced on numerous hosts, varietal resistance of pea and bean, host range, and properties of the viruses in vitro.

Pea streak virus 1 produced a streaking of the stems, petioles, and main veins of the leaves of the pea, but no leaf mottling. All of the alfalfa mosaic viruses produced a leaf mottling, and in addition alfalfa mosaic virus 1B caused a spotting of the leaves and a slight streaking of the stems.

Seventeen varieties of peas were tested with the four viruses. All varieties were susceptible to pea streak virus 1. Horal was the only variety immune to the three alfalfa mosaic viruses. In general, alfalfa mosaic virus 1B produced the severest symptoms of the alfalfa mosaic viruses.

Pea streak virus 1 was not infectious to bean, whereas the alfalfa mosaic viruses produced local necrotic lesions. The Stringless Green Refugee variety was the most susceptible to the three alfalfa mosaic viruses, as determined by total number of lesions produced. Great Northern U. I. No. 1 was next in susceptibility. Corbett and Robust showed about the same tolerance.

The host range of the pea streak virus is more limited than that of the three strains of alfalfa mosaic virus. Pea streak virus 1 did not infect any species outside of the family Leguminosae. The alfalfa mosaic viruses, besides infecting many legumes, also infected *Nicotiana tabacum*, *Petunia hybrida*, *Datura stramonium*, *Cucumis sativus*, and *Zinnia elegans*.

The symptoms produced by the four viruses on certain differential hosts showed distinct differences, making it possible further to distinguish the viruses.

The thermal inactivation point, resistance to aging in vitro, and tolerance to dilution were determined for all of the viruses. The pea streak virus was inactivated between 62° and 65° C. Alfalfa mosaic viruses 1 and 1A were not infectious when heated between 65° and 70° for 10 minutes. Alfalfa mosaic virus 1B was inactivated when heated at 70° to 75° for 10 minutes. Pea streak virus 1 lost its infectivity when aged in vitro for 2 days. The alfalfa mosaic viruses were noninfectious after 4 to 5 days' aging. Pea streak virus 1 tolerated a dilution of about 1 to 5,000. Alfalfa mosaic virus 1 lost its activity at a dilution of about 1 to 2,000 and alfalfa mosaic viruses 1A and 1B at about 1 to 3,000.

Pea streak virus 1 can be separated from a mixture with the alfalfa mosaic viruses by inoculating Horal peas. This variety is susceptible to the pea streak virus but immune to the alfalfa mosaic viruses. No means of separating alfalfa mosaic virus 1 from a mixture with alfalfa mosaic viruses 1A and 1B has been found. The separation of alfalfa mosaic viruses 1A and 1B from each other, as well as from alfalfa mosaic virus 1, can be accomplished by differential host reactions as well as by differences in their properties in vitro.

The differences between the several viruses here reported, as well as between other legume viruses, appear to be sufficient to permit identification and classification.

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STUDIES ON THE CAUSE OF IMMUNITY OF MONOCOTYLEDONOUS PLANTS TO PHYMATOTRICHUM ROOT ROT [1]

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INTRODUCTION

The root rot disease caused by *Phymatotrichum omnivorum* (Shear) Duggar is known to attack 1,708 kinds of plants (*8*).[3] All of these are gymnosperms or dicotyledons. Though some dicotyledonous plants are resistant to root rot, the majority are moderately to extremely susceptible. No monocotyledonous plant, however, has yet been proved to be susceptible to this disease (*7*).

Earlier results (*3*) indicate that this general immunity of monocotyledons to *Phymatotrichum* root rot is associated with a relatively high concentration in their roots of some substance that inhibits the growth of *P. omnivorum*. Little, if any, growth of the fungus occurred in autoclaved, undiluted juices from the roots of four immune monocotyledons, namely, corn (*Zea mays* L.), onion (*Allium cepa* L.), canna (*Canna* sp.), and nutgrass (*Cyperus rotundus* L.). On the other hand, profuse growth was obtained in autoclaved, undiluted juices from cotton (*Gossypium hirsutum* L.), carrot (*Daucus carota* L.), and sweetpotato (*Ipomoea batatas* (L.) Lam.) roots. After the juices had been diluted with distilled water, good growth was obtained in material from both the immune and susceptible plants.

These results have since been confirmed by further tests (*2*) by the same methods. With the dicots, there was again heavy growth in undiluted juices from cotton, sesbania (*Sesbania* sp.), guar (*Cyamopsis psoraloides* (Lam.) DC.), and carrot roots, with less growth as the juices were diluted with distilled water. With the monocots, undiluted juices from onion, nutgrass, and sorghum (*Sorghum vulgare* Pers.) roots nearly or entirely prohibited growth, while diluted juices permitted good growth. However, somewhat aberrant results were obtained with juices from cowpea (*Vigna sinensis* (L.) Endl.) and corn roots. The general nature of the results is shown in part in figure 1. Colonies of *Phymatotrichum omnivorum* here reached the following mean weights in 28 days: In undiluted carrot juice, 593 mg; in carrot juice diluted to one-fourth in distilled water, 242 mg; in undiluted onion juice, no growth; and in diluted onion juice, 181 mg.

Since dilution of juice from monocots permitted growth, the inhibition in the undiluted juice could scarcely have been due to insufficient nutrients. It appears probable instead that specifically

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[2] The writers take pleasure in expressing their appreciation of the advice of Dr. J. J. Taubenhaus, chief of the division of plant pathology and physiology, and Dr. G. S. Fraps, chief of the division of chemistry, in connection with various phases of this work.

[3] Reference is made by number (italic) to Literature Cited, p. 786.

inhibitory materials present in these juices make monocots immune to *Phymatotrichum* root rot.

Without discussing work on the nature of resistance to various plant diseases, recently reviewed at length by Brown (*1*), mention should be made of studies by Moore (*6*) on the rate of growth of *Phymatotrichum omnivorum* in dilute decoctions prepared from dried roots. Decoctions from cotton roots, added to potato-dextrose agar, accelerated growth, while fresh decoctions from corn, wheat, or

FIGURE 1.—Growth of *Phymatotrichum omnivorum* after 4 weeks in juices expressed from carrots (*A*, *C*) and onions (*B*, *D*). *A*, *B*, undiluted juices; *C*, *D*, diluted to one-fourth in distilled water. Note no growth in undiluted onion juice (*B*) and good growth after dilution (*D*).

barley roots generally retarded it. Moore concluded that "water-soluble, labile substances present in the roots of plants immune from the attack of Phymatotrichum have some part in establishing this immunity."

The present paper summarizes studies directed toward isolation and identification of the inhibitory substances in roots of monocotyledonous plants. Certain aspects of this work have been presented previously in abstract form (*5*).

METHODS

The general method of attack has been to attempt to grow the fungus, *Phymatotrichum omnivorum*, on juices expressed from the roots of various plants, and on combinations of juices and fractions of juices with a synthetic nutrient solution. The fungus was grown in small volumes of these liquids in culture tubes. Fractions of plant juices were compared on the basis of the concentrations necessary to inhibit growth. Growth was always successful in check tubes containing the synthetic nutrient solution alone.

In the preparation of the juices, only the underground portions of plants (roots, corms, rhizomes, etc.) were used. These were washed, ground, and the juice expressed with a hand press. The juice was filtered through absorbent cotton and used at once for fractionation as outlined below in presentation of the various experiments. The solvents used in fractionation prevented fungous or bacterial contamination during manipulation, but no protection against changes due to oxidation was attempted.

Final fractions of juices were added to synthetic nutrient solution 70 (*4*), which contains per liter (grams): Ammonium nitrate, 1.18; dextrose, 40; K_2HPO_4, 1.35; $MgSO_4.7H_2O$, 0.75; KCl, 0.15; and $FeCl_3$, 0.0015. The nutrient solution was used in uniform concentration in all the final cultures, while the concentration of the plant juice fraction was varied throughout the range indicated in the tables. In general, the final media were adjusted uniformly to pH 7.0 by the addition of potassium hydroxide when required. Ether-soluble materials, added in ether solution, were usually not neutralized, but were added in relatively minute amounts to the buffered nutrient solution. The media were distributed to culture tubes, and autoclaved at 15 pounds for 20 minutes. Except as otherwise specified, this final autoclaving was the first heating of the material.

Ether-soluble fractions of juices have generally been dispensed while still in ether solution. Individual portions were placed in culture tubes, which already contained 1 cc of the synthetic nutrient solution, and the tubes were warmed at reduced pressure to remove the ether. The remaining 3- or 4-cc portion of nutrient solution was then added to each tube, and the tubes were plugged and autoclaved.

Aqueous fractions of the plant juices were concentrated at reduced pressure, mixed as required with nutrient solution to obtain various concentrations of the plant-juice material, and the mixture was then measured into the culture tubes.

The cultures were inoculated (except in a few experiments) with portions of sclerotial masses of *Phymatotrichum omnivorum* strain 24 taken from flask cultures on synthetic media, and were incubated at room temperature. Observations on possible growth were continued for several months, the tables representing the maximum growth possible rather than growth within a definite period. Lack of growth of the fungus, shown by minus signs in the tables, indicated that a particular dilution of the plant juice was capable of completely inhibiting growth of the fungus. Growth indicated lack of potency. In the tables, a single plus sign represents growth that filled not more than half of the culture solution; two plus signs represent growth that filled most of the culture solution. Cultures were replicated four, five, or occasionally six times, and there was generally little variation in

results within a group of replicates. Some variation was to be expected near the concentration limiting growth of the fungus, particularly with fractions not soluble in water but of necessity tested in the aqueous nutrient solution.

In tabulating the results, the concentrations mentioned for various fractions of the plant juices in the culture solutions refer always to the volume of original plant juice from which the fraction was prepared, without regard to the weight of material in this particular fraction. A fraction containing only a trace of the original dry material was still considered of 1.0 concentration if made up to the volume of the juice prior to fractionation. Similarly, a concentration of 12.0 in the tables means that the final substratum contained a fraction prepared from a volume of plant juice equal to 12 times the volume of the culture solution, even though the culture solution may have contained only 1 percent of the dry matter present in this original juice. The dry weights, given for some of the fractions, refer to grams per 100 cc of the fraction at 1.0 concentration.

EXPERIMENTAL RESULTS

ETHER-SOLUBLE AND AQUEOUS FRACTIONS OF PLANT JUICES

Several preliminary fractionations of various juices may be summarized briefly. Fresh onion juice was treated with phosphotungstic acid, filtered, the filtrate cleared, treated with neutral lead acetate, and the precipitate again removed. Neither precipitate inhibited growth of *Phymatotrichum omnivorum*. The filtrate was deleaded, evaporated to a thick paste, and extracted with absolute alcohol. The extract proved nonpotent in preventing growth of the fungus, while the residue was highly potent. Acetone and ether extracts from the residue were potent. Ether extracts from an aqueous solution of the residue were inhibitory, but even after exhaustive ether extraction which yielded finally nonpotent extracts, the aqueous residue was still potent.

Fresh onion juice was extracted repeatedly with ether, with similar results. A first extract by two portions of ether was highly potent, preventing growth of *Phymatotrichum omnivorum* at a concentration of 1.5. The aqueous residue was acidified with hydrochloric acid and extracted with two more portions of ether, yielding a somewhat less potent fraction, able to prevent growth at 3.0. The aqueous residue was then made alkaline with potassium hydroxide and extracted again, yielding a nonpotent ether fraction. The final aqueous residue was still potent, preventing growth at a concentration of 3.0. These results indicated that onion juice contained both ether-soluble and nonether-soluble materials able to inhibit growth of *Phymatotrichum omnivorum*.

Fresh juice from corn roots was extracted similarly with ether. As with onion, the ether extract (from acidified juice) and the aqueous residue were about equally potent in preventing growth of the fungus.

Some experiments were performed to compare fractions prepared in this way from monocots and dicots. In the series summarized in table 1, the aqueous residue of the juices did not differentiate between susceptible and immune plants. This fraction prevented growth in material from the highly susceptible carrots and from the immune onions. The ether extract, on the other hand, was potent with the onion but did not inhibit growth with juices from either of the dicots.

TABLE 1.—*Inhibitory effect of some fractions of carrot, turnip, and onion juice on growth of Phymatotrichum omnivorum*

Juice and fraction used	Growth (+) or lack of growth (−) in nutrient solution 70 plus the following concentrations[1] of fractions—				
	6.0	3.0	1.5	1.0	0.75
Carrot:					
Complete juice, adjusted to pH 7.0				++	++
Ether extract	++	++	++		++
Aqueous residue	−	−	++		++
Turnip:					
Complete juice, adjusted to pH 7.0				−	−
Ether extract	++	++	++		++
Aqueous residue	−	−	−		−
Onion:					
Complete juice, adjusted to pH 7.0				++	++
Ether extract	−	−	−[2]		−[2]
Aqueous residue	−	−	++		++

[1] Concentrations represent the volume of the original juice from which a portion of the fraction was prepared, divided by the volume of the culture solution in which that portion is tested.
[2] Growth in 1 of 5 tubes.

In other experiments carried out at this time, ether extracts were prepared from juices from cannas, onions, potatoes, sweetpotatoes, carrots, and *Hemerocallis* roots. In sufficiently high concentration, the aqueous residues remaining after ether extraction of all these juices inhibited growth of *Phymatotrichum omnivorum*. On the other hand, the ether-soluble fractions from the juices of the monocots were generally potent, while those from the juices of the susceptible dicots were rarely inhibitory, even when used at high concentration. This suggested that the materials that make monocots immune from root rot might be those present in the ether-soluble fractions of the juices, rather than those in the aqueous fractions which were apparently common to both groups of plants. Further attention was therefore given to the ether fractions.

ETHYL ETHER AND PETROLEUM ETHER FOR SEPARATION OF POTENT FRACTIONS

In experiments with onion juice, canna root juice, and *Hemerocallis* root juice, extraction with ethyl ether was compared with extraction with petroleum ether. In each case ethyl ether extracts were more potent in preventing growth of *Phymatotrichum omnivorum* than extracts with petroleum ether. When the same portion of juice was extracted first with petroleum ether and then with ethyl ether, the ethyl ether fraction was much more potent than the petroleum ether fraction. On the other hand, when juice was extracted first with ethyl ether and then with petroleum ether, all the potent material was extracted by the ethyl ether (table 3). Extraction with ethyl ether was thus more complete and included the materials that might be taken out by petroleum ether. Ethyl ether was therefore used for later extractions.

ACETONE PRECIPITATION OF ETHER-SOLUBLE FRACTIONS

Phospholipins were separated by treating ether extracts with anhydrous acetone in large volume overnight in the refrigerator. The white, greasy phospholipin precipitate obtained from ether extracts

from onion, corn, *Hemerocallis*, and other monocots invariably proved nonpotent (fraction *c*, table 2), while the acetone-soluble materials remaining in the ether-acetone solution (fraction *d*) were as potent in preventing growth of *Phymatotrichum omnivorum* as the original complete ether extract.

TABLE 2.—*Inhibitory effect of some fractions of onion juice on growth of Phymatotrichum omnivorum*

Treatment of the fractions	Percent dry weight [1]	Growth (+) or lack of growth (−) in nutrient solution 70 plus the following concentrations of fractions—						
		12.0	9.0	6.0	3.0	1.5	1.0	0.75
a. Complete juice, at pH 7.0	6.9475						−	−
b. Complete ether extract	.0324	−	−	−	−	−		
Precipitation of *b* with acetone:								
c. Precipitate	.0056	+	+	++	++	++		
d. Acetone-soluble	.0268	−	−	−	−	−		
Saponification of *d* for 2 hours at room temperature:								
e. Nonsaponified	.0223	−	−	−	++	++		
f. Saponified, ether-soluble	.0056	−	−	−	++	++		
g. Saponified, aqueous residue		++	++	++	++	++		

[1] Dry weights refer to grams per 100 cc of the fraction at 1.0 concentration.

SAPONIFICATION WITH ALCOHOLIC POTASSIUM HYDROXIDE

Saponification of ether extracts with alcoholic potassium hydroxide was tried in several experiments. After saponification, water was added and an ether extraction was made which presumably removed nonsaponified materials. The aqueous residue was then acidified with hydrochloric acid, and a second ether extraction was made to remove acidic, saponified materials. The final aqueous residue consisted of saponified materials, soluble in water but not in ether.

Fractionation of onion juice in this way usually yielded results as given in table 2 for one experiment. The nonsaponified fraction (*e*) was reduced in weight and potency by longer treatment, or higher temperatures during saponification, but usually retained some potency. Most of the potency of the saponified material was in the ether-soluble fraction (*f*).

Similar fractionation of the ether-acetone-soluble portion of corn juice yielded different results. The nonsaponified portion lost all potency, but the saponified, ether-soluble fraction was as potent as the material prior to saponification. This apparent discrepancy in saponification of ether fractions from onion and those from other monocot juices was explained in later fractionations in aqueous sodium carbonate solution.

These results indicated that the potency of ether extracts of monocots was due at least in part to saponifiable materials containing an acidic constituent.

FRACTIONATION OF ETHER EXTRACTS BY EXTRACTION WITH AQUEOUS SODIUM CARBONATE SOLUTION

The potency of ether extracts from plant juices was not diminished by repeated washing with distilled water. Washing with relatively small volumes of 1-percent aqueous sodium carbonate solution, how-

ever, caused extreme reduction in potency. For example, an ether extract from canna root juice contained 0.0081 g per 100 cc of the original material, and prevented growth of *Phymatotrichum omnivorum* when present at a concentration of 6.0. After washing twice with sodium carbonate solution and again with distilled water, the dry matter had decreased only to 0.0050 g per 100 cc of the original juice, while no potency was found even at a concentration of 12.0.

TABLE 3.—*Inhibitory effect of some fractions of juice from Hemerocallis roots on growth of Phymatotrichum omnivorum*

Treatment of the fractions	Percent dry weight [1]	Growth (+) or lack of growth (−) in nutrient solution 70 plus the following concentrations of fractions—							
		12.0	9.0	6.0	3.0	1.5	1.0	0.75	0.25
a. Complete juice, at pH 7.0	------	------	------	------	------	------	−	−	++
Extraction with petroleum ether, followed by ethyl ether:									
b. Petroleum ether extract	0.0023	−	[2] +	++	++	++	------	------	------
c. Ethyl ether extract	.0308	−	−	−	++	++	------	------	------
Extraction with ethyl ether followed by petroleum ether:									
d. Ethyl ether extract	.0257	−	−	−	++	++	------	------	------
e. Petroleum ether extract	.0019	++	++	++	++	++	------	------	------
f. Aqueous residue from *d*	------	−	−	−	−	−	------	------	------
Washing *d* with 1 percent sodium carbonate solution:									
g. Residue from *d* after washing	.0115	++	++	++	++	++	------	------	------
h. Ether extract from acidified washings	.0120	−	−	−	[2] ++	++	------	------	------

[1] See footnote 1, table 2.
[2] Growth in 2 of 4 tubes only.

Results typical of those obtained with juices from various monocots are given in table 3 for *Hemerocallis* roots. In this experiment, the complete ethyl ether extract (*d*) was potent enough to prevent growth when at 6.0 concentration. Washing 900 cc of this fraction with two 250-cc portions of 1-percent sodium carbonate solution, and with one 250-cc portion of distilled water, reduced the weight of dry matter in the extract (*g*) by a half and entirely removed the potency. The combined washings were acidified slightly with hydrochloric acid, and extracted with three 100-cc portions of ether. The inhibitory material was recovered in a fraction (*h*) containing less than half the dry matter of *d* but having slightly greater potency.

Similar separations with juices from canna roots, giant reed (*Arundo donax* L.) roots, gladiolus (*Gladiolus* sp.) corms, and Johnson grass (*Sorghum halepense* (L.) Pers.) roots are summarized in table 4. As with *Hemerocallis*, the potent material in the ether fraction was all removed by the aqueous sodium carbonate solution, from which it was recovered by acidification and ether extraction. The final fraction *e* was highly potent, only 0.0174 g of dry matter of canna material per 100 cc of final culture fluid being necessary to inhibit growth of *Phymatotrichum omnivorum*. With all these monocots, the potent materials in the ether extract proved completely soluble in 1-percent sodium carbonate solution.

TABLE 4.—*Inhibitory effect of fractions of juices from some monocotyledonous plants on growth of Phymatotrichum omnivorum*

Treatment of the fractions	Percent dry weight [1]	Growth (+) or lack of growth (−) in nutrient solution 70 plus the following concentrations of fractions—							
		12.0	9.0	6.0	3.0	1.5	1.0	0.75	0.25
Canna root juice:									
a. Complete juice, at pH 7.0							−	[2] −	++
b. Aqueous residue after ether extraction									
c. Complete ether extract	0.0100	−	−	−	−	++			
d. Residue from *c* after washing with sodium carbonate solution	.0020	++	++	++	++	++			
e. Ether extract from acidified washings	.0058	−	−	−	−	++			
Giant reed root juice:									
a. Complete juice, at pH 7.0							[3] Tr.	+	++
b. Aqueous residue after ether extraction					−	−		−	
c. Complete ether extract	.0333	−	−	−	+	++			
d. Residue from *c* after washing with sodium carbonate solution	.0195	+	+	+	++	++			
e. Ether extract from acidified washings	.0153	−	−	[2] −	++	++			
Gladiolus corm juice:									
a. Complete juice, at pH 7.0							−	−	−
b. Aqueous residue after ether extraction						−		−	−
c. Complete ether extract	.0395	−	−	−	++	++			
d. Residue from *c* after washing with sodium carbonate solution	.0212	++	++	++	++	++			
e. Ether extract from acidified washings	.0126	−	[2] −	[3] Tr.	++	++			
Johnson grass root juice:									
a. Complete juice, at pH 7.0							−	−	++
b. Aqueous residue after ether extraction				−	−	−		−	
c. Complete ether extract		−	−	−	[3] ++	[4] ++			
d. Residue from *c* after washing with sodium carbonate solution		++	++	++	++	++			
e. Ether extract from acidified washings		−	−	−	−	[4] ++			

[1] See footnote 1, table 2.
[2] Trace of growth in 1 tube only.
[3] Growth in 2 of 4 tubes.
[4] Abundant growth in 1 tube only.

TABLE 5.—*Inhibitory effect on growth of Phymatotrichum omnivorum of some fractions of onion juice, showing potency of washed ether extract*

Treatment of the fractions	Percent dry weight [1]	Growth (+) or lack of growth (−) in nutrient solution 70 plus the following concentration of fractions—							
		12.0	9.0	6.0	3.0	1.5	1.0	0.75	0.25
a. Complete juice, at pH 7.0							−	−	++
b. Complete ether extract	0.0344	−	−	−	−	−			
c. Residue from *b* after washing with 1-percent sodium carbonate solution	.0206	−	−	−	−	+			
d. Ether extract from acidified washings	.0091	−	−	−	+	++			

[1] See footnote 1, table 2.

Onion juice yielded somewhat different results (table 5). In several trials, a potent fraction was obtained by ether extraction of acidified sodium carbonate solution washings, just as with the other monocots tested. However, the onion fraction *c*, consisting of portions of the ether extract not soluble in aqueous sodium carbonate solution, was invariably highly potent also. Onion juice therefore contains, in addition to the potent sodium carbonate-soluble fraction apparently common to all the monocots tested, another potent ether-soluble fraction not removed by sodium carbonate solution. This explains why saponification yielded different results with onion and with corn

juices. The acidic fraction soluble in sodium carbonate solution was readily saponified in each case. This left with corn juice no potency in the nonsaponified fractions, while with the onions there remained the additional potent fraction, not soluble in sodium carbonate solution and only slowly saponifiable by potassium hydroxide.

SOME OTHER STUDIES ON ETHER FRACTIONS FROM MONOCOTYLEDONOUS PLANTS

Cold Storage of Ether Fractions as Affecting Apparent Potency

Ether fractions from acidified sodium carbonate solution washings were stored on several occasions in stoppered flasks in the refrigerator. One of these was part of fraction *d* of table 5. After 8 months the dry weight of materials in this liquid had dropped to 0.0078 g per 100 cc of the original volume, presumably on account of a light brownish-white precipitate observed on the bottom of the flask. In cultures set up with this stored material, however, the potency was found to have increased so that no growth occurred at a concentration of 3.0. In the cultures shown in table 5, the addition of 0.0273 g of onion material per 100 cc of culture fluid had not inhibited growth, while the addition of a smaller dry weight of the stored material (0.0234 g) was now effective.

Similar results were obtained later with canna root material. The fresh juice was unusually low in potency. The ether extract from the sodium carbonate washings did not inhibit growth of *Phymatotrichum omnivorum* even at a concentration of 12.0, which provided 0.156 percent of plant material in the culture tubes. After storage for 8 days in the refrigerator, this fraction was again tested. The dry weight of the liquid had decreased slightly, but the potency had increased. A concentration of 10.0 provided 0.123 percent of plant material in the cultures, yet completely prevented growth of *P. omnivorum*.

In both cases, during storage of this fraction in the ether solution some change occurred which increased its potency. Oxidation or hydrolysis may have caused both the loss in weight and the increase in potency. The potent materials that prevent growth of *Phymatotrichum omnivorum* in the cultures are possibly produced by oxidation or hydrolysis and may be evidence of the existence of some precursor in the plant, and are not necessarily identical with the material as found in the original roots.

Solubilities of the Sodium Carbonate-Soluble Potent Fraction

Further separation of potent fractions was attempted with ether extracts from several plants by layering with water plus alcohol or acetone. In general, more material and greater potency were obtained in ether-acetone, ether-methyl alcohol, and ether-ethyl alcohol fractions, and little material or potency in the corresponding aqueous acetone and aqueous alcohol fractions.

Potency against Different Strains of Phymatotrichum omnivorum

Most of the experiments summarized here were performed with cultures of *P. omnivorum* strain 24, small portions of sclerotial masses being used as the inoculum. Several other sets of cultures were

set up with inoculum of strain 43 taken from agar slants. The results were the same, indicating that the reactions concerned are probably general for *P. omnivorum* rather than specific for a particular strain of the fungus.

TABLE 6.—*Inhibitory effect on growth of Phymatotrichum omnivorum of fractions of juices from some dicotyledonous plants*

Treatment of the fractions	Percent dry weight [1]	Growth (+) or lack of growth (−) in nutrient solution 70 plus the following concentrations of fractions—							
		12.0	9.0	6.0	3.0	1.5	1.0	0.75	0.25
Beet juice:									
a. Complete juice, at pH 7.0							+	++	++
b. Aqueous residue after ether extraction		−	−	−	−	++			
c. Complete ether extract	0.0106	+	+	++	++	++			
d. Residue from *c* after washing with sodium carbonate solution	.0073	+	+	+	++	++			
e. Ether extract from acidified washings	.0035	++	++	++	++	++			
Carrot juice:									
a. Complete juice, at pH 7.0							++	++	++
b. Aqueous residue after ether extraction		−	−	−	−	−			
c. Complete ether extract	.0735	++	++	++	++	++			
d. Residue from *c* after washing with sodium carbonate solution	.0701	++	++	++	++	++			
e. Ether extract from acidified washings	.0032	++	++	++	++	++			
Potato juice:									
a. Complete juice, at pH 7.0							Tr.	Tr.	+
b. Aqueous residue after ether extraction		−	−	−	−	++			
c. Complete ether extract	.0109	−	Tr.	+	++	++			
d. Residue from *c* after washing with sodium carbonate solution	.0031	++	++	++	++	++			
e. Ether extract from acidified washings	.0080	−	Tr.	+	++	++			
Sweetpotato juice:									
a. Complete juice, at pH 7.0							[2] +	+	++
b. Aqueous residue after ether extraction				−	−	−			
c. Complete ether extract	.0305	Tr.	Tr.	+	++	++			
d. Residue from *c* after washing with sodium carbonate solution	.0274	+	+	++	++	++			
e. Ether extract from acidified washings	.0034	+	++	++	++	++			
Turnip juice:									
a. Complete juice, at pH 7.0							−	−	[2] ++
b. Aqueous residue after ether extraction		−	−	−	−	−			
c. Complete ether extract	.0194	−	−	−	−	−			
d. Residue from *c* after washing with sodium carbonate solution	.0131	−	−	−	−	−			
e. Ether extract from acidified washings	.0064	−	−	−	++	++			

[1] See footnote 1, table 2.
[2] Growth in 2 of 5 tubes only.

COMPARATIVE STUDIES OF PREPARATIONS FROM JUICES OF SOME DICOTYLEDONOUS PLANTS

Since the sodium carbonate-soluble fraction from the ether extract occurred in all the monocots studied, it was of particular interest to find whether this potent fraction occurred also in dicots. Of the plants included in table 6, beets (*Beta vulgaris* L.), carrots, and sweetpotatoes are highly susceptible to root rot, while potatoes and turnips (*Brassica rapa* L.) are only moderately susceptible and belong to families that contain many resistant plants.

With all five plants, the aqueous residues after ether extraction (fraction *b*) were potent in preventing growth of *Phymatotrichum omnivorum*, as in earlier tests in which this fraction proved uniformly

potent. The ether fractions from the three more susceptible plants did not inhibit growth, while ether fractions from potato and turnip gave results similar to those obtained with monocots. With potato, the potency was entirely in the sodium carbonate-soluble fraction (*e*). In the present experiment all the turnip fractions were potent. This does not accord fully with results with another lot of turnip juice as given in table 1 but it does agree with the strong inhibiting effect of turnip juice noted in previous work (*3*).

The difference found here between the more susceptible and the more resistant dicots may be partly quantitative rather than qualitative, at least for the sodium carbonate-soluble fraction. A lower weight of this fraction was obtained from the susceptible dicots here than in corresponding fractions of potato or turnip juice, or of various monocots tested. These results suggest that differences between dicots in susceptibility to root rot may be based on differences in the content of certain ether-soluble materials, which may be of the same nature as those occurring in the immune monocots.

DISCUSSION

The work summarized in this paper has been essentially a gradual fractionation of plant juices, eliminating unimportant fractions by tests in which the root rot fungus itself served as the indicator. Disregarding unsuccessful and relatively unimportant steps, the present status of the fractionation is summarized graphically in figure 2.

Substances capable of inhibiting growth of *Phymatotrichum* in cultures were found among both ether-soluble materials and those remaining in the aqueous residue. The water-soluble portion (*b* of fig. 2) usually included at least 100 times as much of the plant material as the ether extract, and held back growth of the fungus in preparations from all plants studied, whether susceptible or immune. This portion has not yet been investigated extensively for the particular materials to which monocots owe their immunity.

More attention has been given to the ether extract, *c*, which was always potent in separations from monocots but not in those from susceptible dicots. Extraction with aqueous sodium carbonate solution further purified the ether-soluble potent material from the monocots, since materials going into fraction *d* were never potent, except with the onion. The onion contains what is apparently a special potent material, uniformly found in this fraction.

The washed ether extract *d* did not lack potency merely because of dilution. In one experiment with canna root juice, for example, this fraction with a dry weight of 0.0051 g per 100 cc was tested at a concentration of 48.0, making the culture solution contain 0.2448 percent of canna material. No inhibition of *Phymatotrichum* was obtained, although growth was inhibited with a tenth as much of some of the potent ether fractions.

The final fraction *e*, consisting of the potent material recovered from the sodium carbonate solution washings, was usually as potent as *c*, despite the lower dry weight. Except with onion, all the potent material of the ether extract of monocots was contained in this fraction. Relatively small amounts of this final fraction were required to inhibit growth of *Phymatotrichum omnivorum*. Growth was inhibited in cultures that contained less than 0.1 percent dry weight of the plant

material. The concentration necessary ranged from 0.0174 percent in a canna series to 0.0918 percent in a giant reed series.

Growth was prevented with complete canna juice diluted to about 2.25 percent, and with complete onion juice diluted to about 4.5 percent, of dry matter. With the final potent fractions of these juices, growth was prevented with only 0.0174 percent and 0.0546 percent, respectively, of plant material. Substances in these fractions were thus about 130 and 82 times as potent, for the same dry weight, as the original juices.

It may be questioned whether the same type of material was present in fraction *e* from some of the dicots. This fraction generally con-

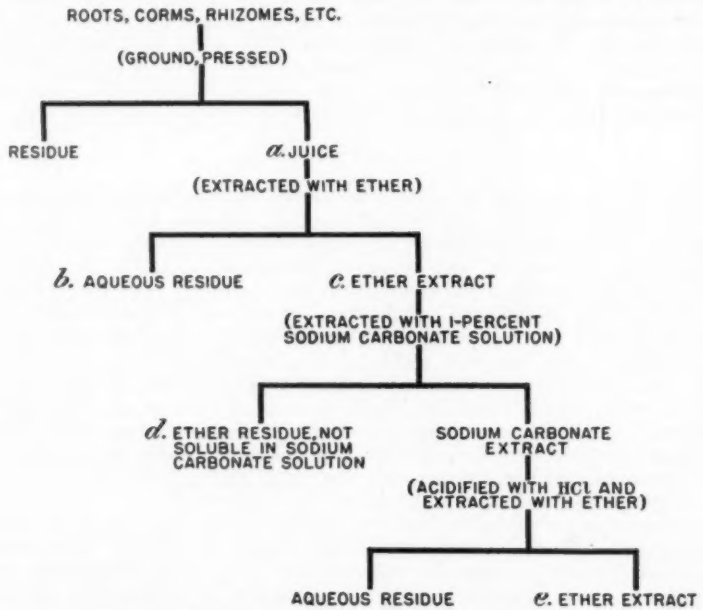

FIGURE 2.—Outline of fractionation of juices of monocotyledonous and dicotyledonous plants, as in experiments summarized in tables 3 to 6. Fractions tested are indicated here by the same letters as in tables 4 and 6.

tained little material. With the potato, a higher yield was obtained and growth of the fungus was inhibited in cultures containing 0.096 percent of the dry material. This may be the same type of material found to be nonpotent in the smaller amounts in other dicots. However, with the turnip a low weight of this fraction (only 0.0384 percent) in the cultures was sufficient to prevent growth of the fungus, which suggests that this turnip fraction might be qualitatively as well as quantitatively different from that of some of the other dicots. These fractions from some of the dicots may be associated with the resistance of various families and species to root rot.

The fractions tested were not exposed to conditions that might produce toxic byproducts not present in the original roots. The separations did not involve reagents likely to produce permanent

chemical changes in the plant materials. Fractionations with ether were followed always by washing with water to remove from the ether solution traces of water-soluble materials. Use of blanks in occasional experiments, and accompanying fractionations of dicot juices, showed that substances inhibiting growth in the cultures were actually from the monocot roots, and were not due to accumulations of traces of chemicals in the juices during manipulation.

By the methods used, roots of immune monocots all yielded an ether-soluble fraction capable of inhibiting the growth of the fungus, while roots of susceptible dicots did not. This fraction *e* (possibly in conjunction with some of the water-soluble inhibitory substances) is probably concerned in the immunity of monocots to root rot. It is then of some interest to consider the possible chemical nature of materials that may be in this fraction. The properties of this fraction are: Solubility in ether, from which it cannot be washed by water nor precipitated by acetone; solubility in aqueous sodium carbonate solution, from which it can be recovered by ether extraction after slight acidification; relative insolubility in petroleum ether as compared to ethyl ether; probable solubility in alcohols. This information is sufficient to exclude the bulkier plant constituents, sugars, proteins, and so on, which would be in the aqueous rather than in the ether fractions. It excludes phospholipins, which would be precipitated by the acetone. It excludes neutral fats or sterols, which would not go into the sodium carbonate solution. The potent fraction presumably consists of definitely acidic, ether-soluble substances, perhaps organic acids or esters.

SUMMARY

Root rot caused by *Phymatotrichum omnivorum* is known to attack 1,708 plants, all gymnosperms or dicots, while monocots are immune. Juices expressed from the roots of monocots contain some material that prevents growth of the fungus, which grows well in similar juice from susceptible dicots.

Ether extracts of juices from roots of monocots were potent in preventing growth of the fungus, while those from roots of susceptible dicots were not potent. The aqueous residues of juices from susceptible as well as from immune plants proved potent when tested in the culture solutions.

In ether extracts from all monocots tested, potent material has been found in a fraction characterized by the following properties: Solubility in ether, from which it cannot be washed by water nor precipitated by acetone; solubility in aqueous sodium carbonate solution, from which it is recovered in ether after slight acidification; relative insolubility in petroleum ether as compared to ethyl ether; probable solubility in alcohols. Fractions of this kind, which were approximately 100 times as potent on a dry-matter basis as the original juice, completely prevented growth of *Phymatotrichum omnivorum* when added to nutrient solutions in amounts that supplied from 0.02 percent to 0.09 percent of plant material. Such fractions were prepared from onion bulbs, gladiolus corms, and giant reed, canna, *Hemerocallis*, and Johnson grass roots.

Onion juice, which was studied in many experiments, was found to contain an additional potent fraction, insoluble in sodium carbonate

solution but apparently slowly saponifiable in alcoholic potassium hydroxide.

Ether fractions from susceptible dicotyledonous plants, such as carrots, beets, and sweetpotatoes, were uniformly nonpotent. However, the less susceptible potato and turnip yielded potent ether fractions. These fractions may be associated with differences in the susceptibility to root rot of various families and species of dicots.

The general immunity of monocots to root rot is due at least in part to the presence in the roots of these plants of minute quantities of acidic, ether-soluble substances, possibly organic acids or esters.

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A MEASURE OF TOXICITY IN PLANT STUDIES[1]

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The toxicity of a compound for a plant is usually expressed in terms of the minimum concentration of the compound required to kill the plant. Other standards of toxicity frequently used are the minimum concentration that prevents lengthening of the primary root of young

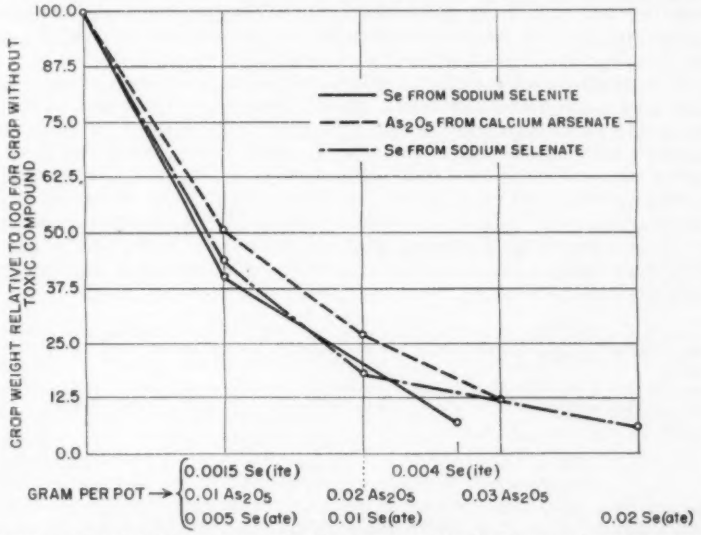

FIGURE 1.—Growth of millet in quartz sand with increasing quantities of calcium arsenate, sodium selenate, and sodium selenite.

seedlings and the concentration required to produce certain symptoms, such as chlorosis. Although these standards are adequate for many investigations, they are not entirely satisfactory for quantitative studies of toxicity, particularly where it is desired to measure the influence of some factor on toxicity. The end points are not sufficiently sharp.

The indefiniteness of the end point, concentration killing the plant, is shown by the curve for decreasing growth with increase in the toxic compound. Figure 1 shows how, in pot experiments, the growth of millet (*Setaria italica*) in quartz sand is affected by three toxic compounds—sodium selenate, sodium selenite, and calcium arsenate. The selenate curve represents the average of results obtained in 11 different experiments, except the point at 0.02 Se, which is a single determination. The selenite curve is an average of three experiments and the arsenate curve an average of nine experiments. All three curves are

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of the same form. Probably this form holds for toxic substances in general when there is no interaction between the toxic substance and substances in the medium of growth. It is obvious from the gradual approach of the growth curve to the abscissa that a high order of experimental accuracy is needed to locate exactly the point of no growth (killing concentration).

A more satisfactory measure of toxicity is the quantity or concentration of toxic compound required to reduce growth one-half. This is a quite obvious criterion of toxicity that has been used by the writer [2] and probably by others. Apparently it should be in general use. The value is determined by growing plants with and without the toxic compound, plotting weight of crop against quantity of toxic compound, and locating the critical quantity of toxic compound from the curve. This measure of toxicity has a sharp end point. Figure 1 shows that at 50 percent of normal growth a small difference in the dose of a toxic compound produces a measurable difference in growth. Moreover, the toxicity curve shows that if the critical quantity of toxic compound is known approximately, the half value may be determined quite exactly by interpolation when only two or three differently treated lots of plants are grown. One lot of plants without the toxic compound and one or two lots with the compound are sufficient. Other advantages of the half value as a measure of toxicity are apparent in the data in table 1.

TABLE 1.—*Quantities of calcium arsenate, sodium selenate, and sodium selenite required to reduce growth of millet one-half in quartz sand, as determined at different times*

Calcium arsenate				Sodium selenate				Sodium selenite			
Date of planting	Duration of growth	Weight per pot of plants receiving no arsenate	Arsenate, as As_2O_5, required per pot to reduce growth one-half	Date of planting	Duration of growth	Weight per pot of plants receiving no selenate	Selenate, as Se, required per pot to reduce growth one-half	Date of planting	Duration of growth	Weight per pot of plants receiving no selenite	Selenite, as Se, required per pot to reduce growth one-half
	Days	*Grams*	*Gram*		*Days*	*Grams*	*Gram*		*Days*	*Grams*	*Gram*
Mar. 7	30	4.15	0.010	Jan. 14	42	3.60	0.0043	Sept. 1	23	3.16	0.0014
Mar. 24	31	3.29	.009	Feb. 11	35	3.12	.0054	Oct. 12	32	2.31	.0012
Apr. 17	25	2.67	.011	Feb. 27	35	2.09	.0041	Oct. 31	42	2.18	.0013
Apr. 21	26	2.74	.010	Apr. 1	30	2.90	.0038				
May 20	30	2.22	.011	May 24	25	4.03	.0042				
Aug. 8	25	3.74	.009	June 20	18	2.28	.0043				
Aug. 18	25	2.73	.009	Aug. 29	28	2.66	.0037				
Sept. 10	33	2.17	.012	Sept. 21	23	3.16	.0087				
Dec. 9	42	1.22	.012	Oct. 11	35	1.61	.0046				
				Oct. 12	32	2.31	.0053				
				Oct. 15	33	3.09	.0047				
Average			.010	Average			.0044	Average			.0013
Standard deviation			.0012	Standard deviation			.00056				
Coefficient of variability			12 percent	Coefficient of variability			13 percent				

Table 1 shows half-toxicity values obtained for calcium arsenate, sodium selenate, and sodium selenite in quartz sand with millet as the test crop. The nine determinations for calcium arsenate are replicates, except that they were made at different times of the year, and

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some of them in different years. This applies also to the 11 determinations for sodium selenate and the 3 for sodium selenite. It should be pointed out that these repetitions were not made with the idea of testing the accuracy of the toxicity determination. Millet was grown in pots in quartz sand, with and without a toxic compound, in a large number of experiments, to serve as a standard for comparing other data. It should also be understood that all determinations made in the course of several years are included in the table, except one obviously wrong, and that no attempt was made to secure the highest accuracy in these determinations. The plants were grown in 1-gallon pots and each treatment was in triplicate only.

The determinations of the toxicity values agree closely. This is surprising, for they were made at different times of the year when light and temperature conditions of the greenhouse varied markedly. The marked variability of growth conditions in general is shown by the comparative weights of the plants receiving no toxic compound in relation to the number of days the plants were grown. At different seasons the plants were grown for different lengths of time in order that they might be at approximately the same stage of maturity, the joint stage, when cut.

Apparently, this toxicity value is independent of ordinary variations in light and temperature. Since toxicity determinations, shown in table 1, have a variability of only 13 percent, differences in light and temperature, such as occur in a greenhouse from summer to winter, could not affect the half-toxicity value by more than this amount. Even this small variation is evidently not due to different growth conditions but to experimental error. For three toxicity values of sodium selenate had probable errors averaging ± 0.0006 g, as near as could be calculated; whereas the standard deviation for the sodium selenate values is ± 0.00056 g. In other words, the probable error of a determination accounts for the deviation from the average.

Prior to obtaining the above results it was thought that the toxicity value should vary with general growth conditions, for it seemed that the plants injured by arsenate or selenate should be affected differently from normal plants by changes in growth conditions. Evidently, however, normal plants and plants injured by arsenate or selenate have their growths altered in exactly the same proportion by changes in light and temperature. The toxicity values are, of course, not independent of all changes in growth conditions. Certain changes in nutrient salts, alteration in the sand medium, and variation in the method of applying the toxic compound may alter a toxicity value appreciably.

SUMMARY

It is suggested that the toxicity of a compound for a plant be measured by the quantity or concentration of the compound required to reduce growth by one-half.

This measure of toxicity can be determined with accuracy, since in the region of 50-percent reduction in growth a small difference in the dose of toxic compound produces a measurable difference in growth.

An advantage of this toxicity value is that it is independent of the marked differences in light and temperature that occur in an ordinary greenhouse between summer and winter.

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